

1 Separating cognitive and motor processes in the behaving mouse

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14 15 16 17 **Abstract**

18 The cognitive processes supporting complex animal behavior are closely associated with ubiquitous movements
19 responsible for our posture, facial expressions, ability to actively sample our sensory environments, and other
20 critical processes. These movements are strongly related to neural activity across much of the brain and are often
21 highly correlated with ongoing cognitive processes, making it challenging to dissociate the neural dynamics that
22 support cognitive processes from those supporting related movements. In such cases, a critical issue is whether
23 cognitive processes are separable from related movements, or if they are driven by common neural mechanisms.
24 Here, we demonstrate how the separability of cognitive and motor processes can be assessed, and, when separable,
25 how the neural dynamics associated with each component can be isolated. We establish a novel two-context
26 behavioral task in mice that involves multiple cognitive processes and show that commonly observed dynamics
27 taken to support cognitive processes are strongly contaminated by movements. When cognitive and motor
28 components are isolated using a novel approach for subspace decomposition, we find that they exhibit distinct
29 dynamical trajectories. Further, properly accounting for movement revealed that largely separate populations of
30 cells encode cognitive and motor variables, in contrast to the ‘mixed selectivity’ often reported. Accurately isolating
31 the dynamics associated with particular cognitive and motor processes will be essential for developing conceptual
32 and computational models of neural circuit function and evaluating the function of the cell types of which neural
33 circuits are composed.
34

35 **Introduction**

36 Goal-directed behavior follows from an interplay between cognitive and motor processes in the mammalian brain.
37 For example, while dribbling down the court, a basketball player must track the players around them, decide which
38 play to run, plan their next move, execute fast and accurate movements, and flexibly adapt those movements
39 according to the actions of other players. The neural representations of these cognitive and motor processes are
40 often distributed across many of the same brain areas¹⁻⁶ and engaged concurrently⁷⁻⁹. For these reasons,
41 disentangling the neural signatures of specific cognitive and motor processes is challenging.

42 Many behavioral tasks are designed with this issue in mind, aiming to isolate constituent neural processes by
43 separating them into discrete temporal epochs. For example, in sensory-guided decision-making tasks, subjects are
44 often trained to withhold responses while stimuli are presented so that perceptual decision making is isolated in
45 time from associated actions. Analogous paradigms have been developed to uncover the neural underpinnings of
46 working memory¹⁰⁻¹², motor planning^{13,14}, contextual encoding^{15,16}, reward prediction^{17,18}, and other cognitive
47 processes¹⁹⁻²².

48 These paradigms often rely on the assumption that experimental subjects withhold motor output during task epochs
49 in which instructed responses are absent. However, uninstructed movements not required for task completion – such
50 as changes in posture, facial expressions, and gaze – are commonly observed in rodents, humans, and non-human
51 primates during learned behavioral tasks²³⁻²⁹. Importantly, uninstructed movements explain much of the variance
52 observed in brain-wide neural activity^{27,30-32} and can be strongly correlated with task variables^{12,28,33-38}.

53 These observations imply a serious challenge for experimental studies addressing a wide-ranging set of cognitive
54 processes. If uninstructed movements are correlated with a latent cognitive variable of interest – a stimulus
55 perceived, a decision made, a memory stored, or a motor plan formed – then the neural dynamics leading to, or
56 resulting from, uninstructed movements can be easily misconstrued as responsible for that cognitive process. One
57 common approach to isolate putative cognitive dynamics is to track and ‘regress out’ movements^{24,30,39-44}, but this
58 approach assumes that cognitive and motor processes are separable - that is, driven by independent neural dynamics.
59 However, some cognitive processes may be inherently embodied such that their associated neural dynamics are
60 linked to overt movement^{45,46}. Regressing out neural dynamics associated with embodied movements would lead to
61 the inadvertent removal of the precise dynamics one wishes to study. Whether cognitive and motor dynamics are
62 separable remains an open question and likely depends on the brain area, behavior, and cognitive process of interest.
63 Effective methods both for evaluating separability within specific experimental paradigms and for effectively
64 dissociating cognitive and motor dynamics, when separable, are lacking.

65 Here, we address the separability of dynamics associated with cognitive processes and correlated movements. We
66 developed a behavioral paradigm in which mice perform sensory-guided movements involving multiple cognitive
67 signals in which they often exhibit idiosyncratic, task-correlated uninstructed movements. We build upon work
68 demonstrating how different neural processes can be multiplexed in a single brain region^{39,40,47-50} to develop a novel
69 method for assessing whether cognitive dynamics can be separated from those associated with movements – and
70 for isolating each component, when they are separable. This approach is simple to adopt and does not require
71 tracking or segmentation of body parts. It also does not require an explicit choice of models relating neural dynamics
72 to movement, avoiding common assumptions of linearity. We find that some cognitive signals are separable from
73 dynamics associated with co-occurring movements while others are largely inseparable. When dynamics are
74 separable, examining the component of neural dynamics unrelated to movement revealed trajectories that differed
75 in notable ways from estimates of the same dynamics when corrupted by uninstructed movements. Strikingly, we
76 found that cognitive and motor dynamics were largely encoded by separate populations of cells when uninstructed
77 movements were accounted for. Together, these results highlight the importance of critical consideration of the
78 relationship between cognition and movement to better understand the neural dynamics supporting complex
79 processes and how they map onto the myriad cell types comprising neural circuits.

80 **Results**

81 **Task-switching behavioral paradigm**

82 We first designed a behavioral paradigm associated with multiple cognitive processes. In this paradigm, head-fixed
83 mice performed two directional licking tasks that alternated block-wise within each behavioral session. These tasks
84 varied in their cognitive demands but required the same instructed motor output.

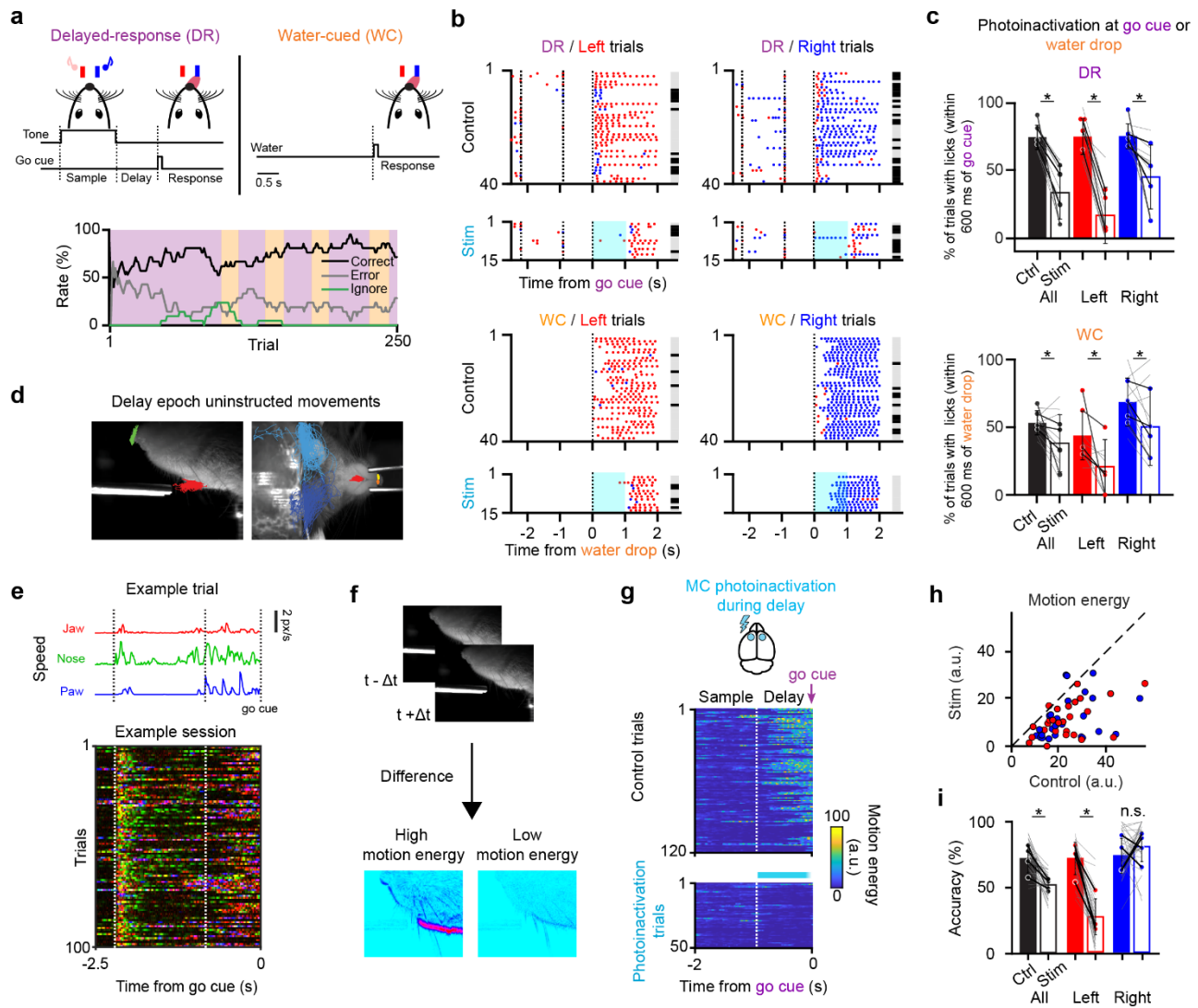
85 This paradigm employed an established delayed-response task (DR) in which motor planning is temporally
86 dissociated from movement execution¹⁴ (**Fig. 1a**). In the DR task, an auditory stimulus indicated the location of a
87 reward. After a brief delay epoch with no auditory stimuli, a separate auditory ‘go cue’ instructed the mouse to
88 move. If the mouse performed a directional tongue movement to the correct target, a water reward was delivered.
89 In separate blocks of trials, mice performed a water-cued (WC) task in which all auditory stimuli were omitted.
90 Instead, a drop of water was presented at a random point in time at a randomly selected reward port. Animals
91 consumed water upon its presentation. Mice received no explicit cues signaling DR and WC blocks. The DR task
92 required a perceptual decision that guides the planning of a subsequent motor action. In the WC task, uncertainty
93 in the timing and location of reward prevented formation of a motor plan prior to reward presentation, and instead,
94 mice detected reward availability using olfactory and/or vibrissal cues⁵¹. This structure required animals to maintain
95 an internal representation of the current block identity (context) to maintain high task performance.

96 We examined uninstructed movements in this behavioral paradigm using high-speed video. We tracked movement
97 of the tongue, jaw, nose, and paws⁵² and calculated instantaneous motion energy to quantify movement in a feature-
98 agnostic manner³¹ (**Fig. 1d-f**). We found that mice performed uninstructed movements that varied in their identity
99 and timing across both trials and contexts (**Fig. 1e** and **Supplementary Movie 1**).

100 Prior work has established the necessity of the antero-lateral motor cortex (ALM) and tongue-jaw motor cortex
101 (tjM1) for the planning and execution of tongue movements^{14,53-56}. To assess cortical involvement in the initiation
102 of instructed movements (directional licking) in both behavioral tasks, we used optogenetic photoinactivation to
103 inhibit the ALM and tjM1 at the go cue (DR) or water presentation (WC) bilaterally in VGAT-ChR2-EYFP mice
104 (10 sessions, 4 mice). Simultaneous photoinactivation of both regions at the go cue (DR task) or water drop (WC
105 task) impaired the initiation of movement in both contexts (**Fig. 1b,c**; DR trials: $41 \pm 20\%$ reduction, mean \pm s.d.,
106 $p = 1 \times 10^{-4}$; DR left trials: $58 \pm 19\%$, $p = 4 \times 10^{-6}$, DR right trials: $30 \pm 28\%$, $p = 7 \times 10^{-3}$; All WC trials: $15 \pm 20\%$, p
107 $= 0.04$; WC left trials: $23 \pm 24\%$, $p = 0.01$, WC right trials: $18 \pm 23\%$, $p = 0.03$; paired t -tests; **EDFig. 1c,d**). To
108 assess cortical involvement in the expression of uninstructed movements, and whether these movements might be
109 controlled by ALM or tjM1 preferentially, we bilaterally silenced the ALM and tjM1 during the delay epoch of DR
110 trials individually (ALM: 15 sessions, tjM1: 9 sessions, 4 mice). Uninstructed movements were suppressed by
111 photoinactivation of either area (**EDFig. 1b**; ALM: $53 \pm 31\%$ reduction, mean \pm s.d., $p = 3 \times 10^{-4}$; tjM1: $62 \pm 24\%$
112 reduction, $p = 2 \times 10^{-3}$, paired t -test) and more strongly suppressed by concurrent photoinactivation of both areas
113 (**Fig. 1g-h**; 29 sessions, 4 mice; $73 \pm 35\%$ reduction, mean \pm s.d., $p = 7 \times 10^{-9}$, paired t -test), similar to previous
114 observations³⁴ (but see ref⁵⁷). In the DR task, delay photoinactivation of both areas led to a significant decrease in
115 overall performance (**Fig. 1i**; $22\% \pm 14\%$ reduction, mean \pm s.d., $p = 2 \times 10^{-6}$ paired t -test; **EDFig. 1b**) as expected
116 from the disruption of choice/planning dynamics¹⁴, often leading to animals responding consistently to a preferred
117 side rather than in a manner commensurate with the sensory cue. These results indicate that both the ALM and
118 tjM1 are involved in the generation of uninstructed movements and the planning and execution of instructed
119 directional tongue movements in the two-context paradigm.

120 Neural dynamics related to task variables

121 While movement- and task-related information is encoded in both the ALM and tjM1 in the DR task^{53,58} and other
122 directional licking tasks⁵⁵, task variables are more strongly represented in the ALM^{55,56,59} and so we focused our
123 subsequent analyses there. We recorded activity extracellularly in the ALM with high-density silicon probes during
124 the two-context paradigm to track dynamics associated with planning, context, and the execution of movements
125 (**Fig. 2**; two-context paradigm: 12 sessions, 6 mice, 522 units including 214 well-isolated single units; an additional
126 3 mice were trained only on the DR task totaling 25 sessions, 9 mice, 1651 units including 483 well-isolated single
127 units included in analyses of the DR task only; see **EDFig. 2a** for per-session statistics). In the DR task, we found
128 that choice selectivity (right vs. left DR trials) was widespread across all task epochs as expected (sample: 36%;
129 delay: 42%; response: 58% of 483 single units, 25 sessions, 9 mice, 483 single units; see **Methods**). Individual units
130 showed a variety of activity patterns across trial types, including delay epoch preparatory activity preceding
131 instructed movements, often taken to be a signature of motor planning^{54,60} (**Fig. 2b left**). Individual units were also
132 selective for behavioral context during all task epochs, including during the inter-trial interval (ITI) (39% of single
133 units, 12 sessions, 6 mice, 214 single units; see **Methods**), suggesting persistent coding of context (**Fig. 2b, right**).



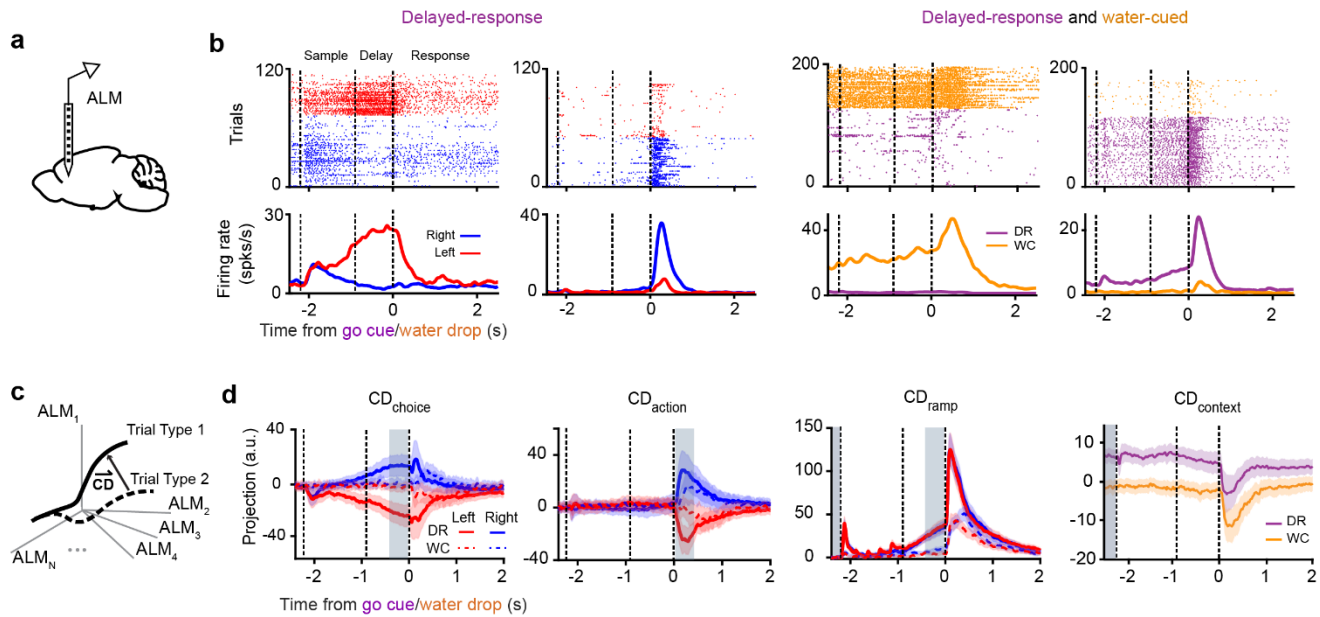
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Figure 1 – Cortical dependence and uninstruced movements during a two-context task. **a. Top**, Schematic of the two-context task. In delayed-response (DR) trials, an auditory stimulus was presented during the sample epoch (1.3 s) instructing mice to lick for reward to the right (white noise) or left (8 kHz tone). Mice were trained to withhold their response during a delay epoch (0.9 s) and initiated their response following an auditory go cue. In WC trials, mice were presented with a water reward at a random port at random inter-reward intervals. The WC task was introduced once mice became experts in the DR task. **Bottom**, 20-trial trailing average of correct, error, and ignore rates for an example session. **b**. Performance for an example session separated by trial type (left vs. right), control vs. photoinactivation trials, and by context. Photoinactivation (1 s) was initiated at the go cue. Blue dots indicate right licks and red dots indicate left licks. Grey bars, correct trials; black bars, error trials. **c**. Percent of trials with correct licks within 600 ms of the go cue on photoinactivation trials. Colored points represent mean values across animals ($n = 4$, individual animals connected by dark lines). Light gray lines denote individual sessions ($n = 10$). Bars are across-session means. Asterisks denote significant differences ($p < 0.05$) between control and photoinactivation trials (All DR trials: $p = 0.0001$; DR left trials: $p = 4.5e-06$; DR right trials: $p = 0.0074$; All WC trials: $p = 0.0371$; WC left trials: $p = 0.0134$; WC right trials: $p = 0.0316$, paired t -test). Error bars denote standard deviation across sessions. **d**. Behavior was tracked with high-speed video from side (left) and bottom (right) views. Trajectories of delay epoch uninstruced movements from an example session overlaid. **e**. Uninstruced movements are highly variable across trials and across time. **Top**, jaw, nose, and paw speed for an example trial. **Bottom**, feature overlay for a subset of trials in an example session. At each time bin, t , an $[r, g, b]$ color value was encoded as $[jaw_t, nose_t, paw_t]$. **f**. Schematic of motion energy calculation. Example frames depicting high and low motion energy are shown. **g-i**. Bilateral motor cortex photoinactivation during the delay epoch. **g**. Motion energy on control (top) and photoinactivation (bottom) trials for an example session. On photoinactivation trials, light was delivered for 0.8 seconds beginning at the start of the delay epoch. **h**. Average delay epoch motion energy on single sessions for control and photoinactivation trials ($n = 29$ sessions, 4 mice). Red points indicate left trials and blue points indicate right trials for a single session. **i**. Performance for control and delay epoch photoinactivation trials. Mice often defaulted to a right choice following delay epoch photoinactivation. Asterisks denote significant differences ($p < 0.05$) between control and photoinactivation trials ($n=29$ sessions, 4 mice). Black lines and points indicate averages across sessions for individual animals and light grey lines indicate sessions.

158 We next sought to understand how the selectivity patterns observed in individual cells were encoded at the
 159 population level. We examined neural activity in state space, in which the firing rate of each unit represents one
 160 dimension. We defined one-dimensional coding directions (CD) within the high-dimensional state space that best
 161 encoded task variables^{54,61–63} (**Fig. 2c**). We first examined putative neural correlates of three cognitive processes –
 162 choice, urgency, and contextual encoding.

163 We defined a coding direction for left-right trial type, CD_{choice} , as the direction in state space that best differentiates
 164 activity on left versus right trials during the delay epoch of DR trials. Projections along CD_{choice} revealed that choice
 165 selectivity in the ALM emerges early in the sample epoch and continues to grow throughout the delay epoch before
 166 decaying at the onset of the response epoch (**Fig. 2d**). Choice could be reliably decoded from projections along
 167 CD_{choice} across sessions (**EDFig. 2c**; AUC: 0.86 ± 0.11 mean \pm s.d.). Such preparatory activity is predictive of
 168 animals' upcoming instructed responses^{13,54,58,61,64,65} and has been taken to represent a neural correlate of a motor
 169 plan^{54,60} or choice^{32,62,66}. We next defined CD_{ramp} as the direction that captures trial-type independent increases or
 170 decreases in preparatory activity between the onset of the stimulus and the go cue in DR trials^{61,62,67,68}. This non-
 171 selective ramping has been thought to represent an urgency or timing signal^{69–72}. Finally, we defined $CD_{context}$, the
 172 direction that best differentiates activity during the inter-trial interval of DR and WC trials (see **Methods**).
 173 Projections along $CD_{context}$ revealed that context is encoded in the ALM throughout each trial (**Fig. 2d**) with strong
 174 modulation at the onset of the response epoch.

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177 **Figure 2 – Single cell activity and population dynamics encode task-relevant cognitive and motor processes.** **a.** Schematic of silicon
 178 probe recordings in the anterolateral motor cortex (ALM). **b.** Spike rasters (*top*) and peri-stimulus time histograms (PSTH; *bottom*) for four
 179 example units in the ALM. Units show selectivity for trial type (left vs. right) and context (DR vs. WC) during all task epochs. PSTHs for
 180 DR and WC tasks shown on right are averages of equal numbers of left and right trials. **c.** Schematic illustrating identification of coding
 181 directions (CD). Coding directions are defined as directions in state space that maximally separate activity between trajectories defined by
 182 trial types (CD_{choice} , CD_{action}), context ($CD_{context}$), or time points (CD_{ramp}). **d.** Projections along each of four defined CDs. Gray shaded
 183 regions indicate time points used for CD estimation. Mean and 95% confidence intervals of bootstrapped distributions shown.

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185 In addition to neural activity putatively related to these cognitive processes, we also examined neural signals
 186 associated with the execution of movements. We defined an additional coding direction, CD_{action} , as the direction
 187 that captures trial-type selective changes in neural activity that emerge after the go cue. Projections of neural activity
 188 along CD_{action} robustly encoded movement direction in the ALM, as expected. Together, these four coding
 189 directions explained $53 \pm 11\%$ (mean \pm s.d.) of the variance in trial-averaged neural data (**EDFig. 2b**). We focus our
 190 analyses on these four population-level signals, which putatively encode ALM dynamics associated with cognitive
 191 and motor processes in the two-context task-switching paradigm.

192 **Uninstructed movements related to preparatory dynamics**

193 We next examined uninstructed movements in the DR task and their correlation with both task variables and
194 preparatory dynamics (**Fig. 3**). We found that animals frequently performed uninstructed movements that were
195 correlated with trial type (**Fig. 3a**) and time within each trial. On single trials, upcoming choice could be decoded
196 from uninstructed movements beginning immediately after the presentation of the sample tone, with accuracy
197 increasing throughout the delay epoch (**Fig. 3b**).

198 Not only were uninstructed movements related to the animal's upcoming actions, but they were highly correlated
199 with preparatory dynamics on a trial-by-trial and moment-by-moment basis. The onset and magnitude of
200 uninstructed movements often coincided with the onset and magnitude of choice selectivity and ramping (**Fig. 3c,e**).
201 We used cross-validated multiple linear regression to predict projections along CD_{choice} and CD_{ramp} on a trial-by-
202 trial basis from captured kinematic features of movement. Model predictions were often highly correlated with
203 motor planning signals, indicating a close relationship between animals' uninstructed movements and preparatory
204 dynamics (**Fig. 3d,f**; CD_{choice} : $R^2 = 0.41 \pm 0.23$, mean \pm s.d across sessions, CD_{ramp} : $R^2 = 0.48 \pm 0.23$, $n = 25$
205 sessions), although this relationship was variable across animals and sessions (**Fig. 3d,f,i bottom row**) and variable
206 in the kinematic features that were most predictive (**EDFig. 3a-c**). This variability is consistent with other studies⁷³
207 and highlights the need for analytical methods for assessing the relationship between neural signals and related
208 movements on a session-by-session basis.

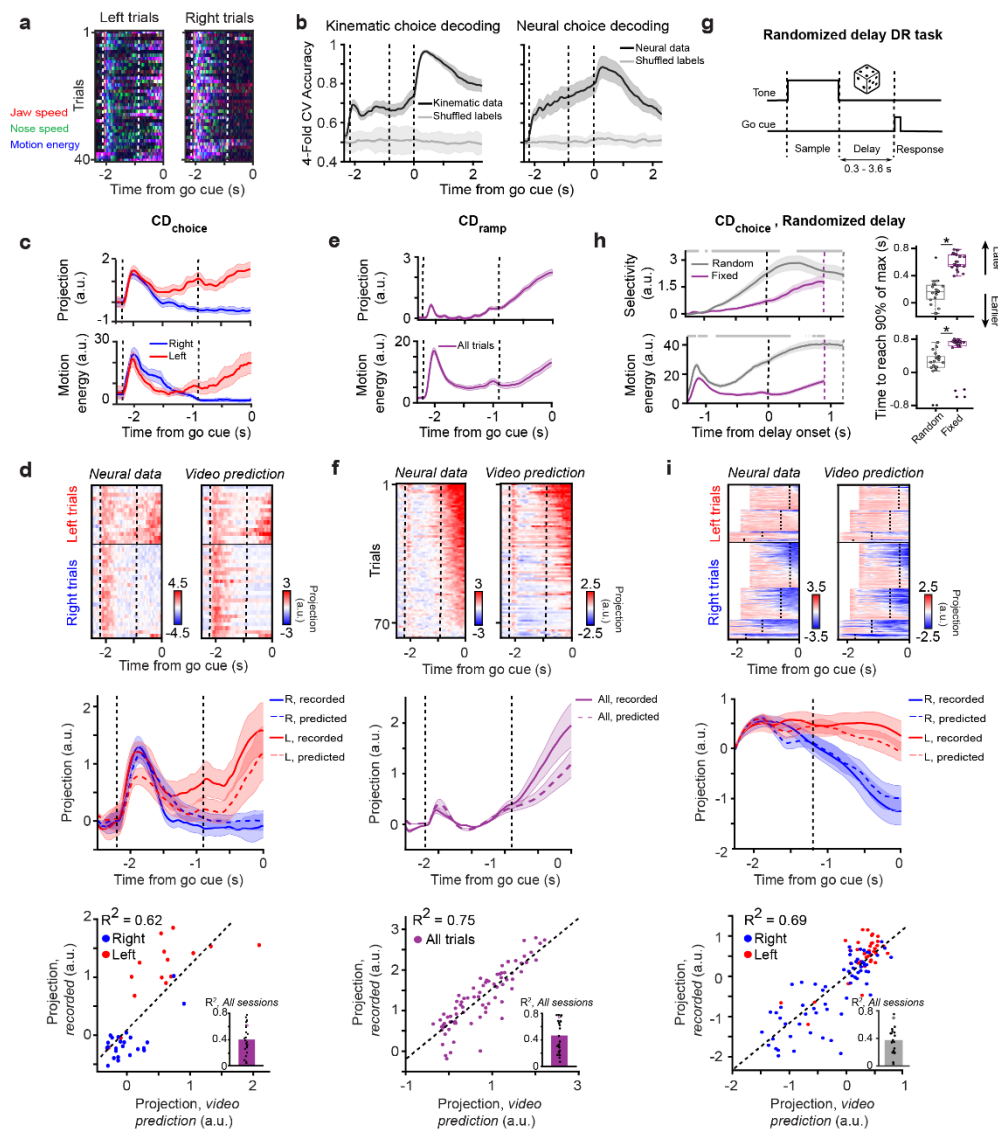
209 To further understand the relationship between uninstructed movements and preparatory dynamics, we trained
210 additional animals on a randomized delay task in which the timing of the go cue cannot be anticipated⁶⁵.
211 Incorporating uncertainty into the length of the delay epoch leads to a qualitative change in population-level choice
212 selectivity. Selectivity in CD_{choice} projections emerges earlier than in the standard fixed-delay DR task (**Fig. 3h top**
213 *right*; fixed: 0.61 ± 0.11 s from delay onset, $n = 25$ sessions; randomized: 0.16 ± 0.19 s, $p = 2.4 \times 10^{-12}$, $n = 19$
214 sessions, two-sided t -test; **Fig. 3h, top left**), suggesting that motor plans are prepared prior to the earliest possible
215 go cue time⁶⁵. We found that the timing of uninstructed movements, too, shifted in an analogous fashion (**Fig. 3h,**
216 *bottom*; fixed: 0.58 ± 0.43 s from delay onset; randomized: 0.19 ± 0.39 s, $p = 0.01$, two-sided t -test). Projections
217 along CD_{choice} remained predictable from uninstructed movements on a single-trial level (**Fig. 3h**; average R^2 across
218 sessions: 0.38 ± 0.20 , $n = 19$ sessions), providing further evidence of the tight link between preparatory dynamics
219 and uninstructed movements.

220 **Uninstructed movements related to behavioral context**

221 We next compared uninstructed movements across task blocks in the two-context paradigm (**Fig. 4**). We found that
222 animals perform qualitatively different uninstructed movements in each behavioral context, despite both contexts
223 requiring instructed movements to the same targets (**Fig. 4a**). Context could be decoded from kinematic features of
224 movement across epochs – including during the ITI, in which external contextual cues were absent (**Fig. 4b,**
225 *left*). The time-course of context decoding from neural population data and from movement kinematics was also
226 similar (**Fig. 4b, right**).

227 We sought to understand whether trial-to-trial variability in the neural representation of context-encoding could be
228 predicted from uninstructed movements. We again trained a multiple linear regression model to predict single-trial
229 projections along CD_{context} from kinematic features and found that, like putative choice and urgency dynamics,
230 context-selective signals could be predicted with high fidelity (**Fig. 4c,d**; $R^2 = 0.49 \pm 0.22$, $n = 12$ sessions).

231 Taken together, these findings suggest that dynamics along CD_{choice} , CD_{ramp} , and CD_{context} could be associated with
232 uninstructed movements and/or the cognitive processes related to the anticipation and planning of upcoming
233 instructed movements and encoding of task context.



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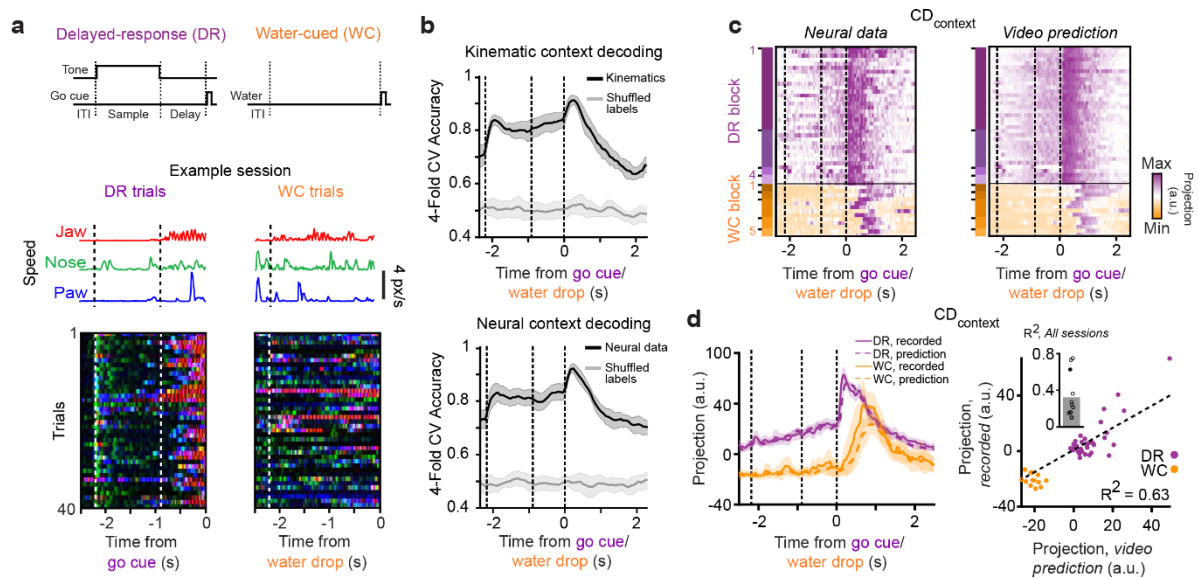
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Figure 3 - Uninstructed movements are tightly linked to putative planning dynamics. **a.** Choice-dependent uninstructed movements. Overlaid trajectories from a random subset of DR trials in an example session. In this example, uninstructed movements are prominent on left, but not right, trials during the delay epoch. **b.** Choice (left vs. right) decoding from kinematic features and neural population data. Gray lines denote shuffled choice labels. **c.** *Top*, average projection onto CD_{choice} on left (*red*) and right (*blue*) trials for the example session depicted in (a). *Bottom*, average motion energy for all correct left and right trials. **d.** Observed and video predictions of single-trial projections of neural activity onto CD_{choice} (see **Methods**) for the same example session as in (a). *Top*, Heatmap of observed and predicted single-trial projections. Trials are sorted by the observed average projection magnitude in the late delay, with left and right trials sorted separately. *Middle*, trial-averaged CD_{choice} projections and predictions. *Bottom*, scatter plot of the average delay epoch projection of neural data onto CD_{choice} versus corresponding video predictions. Dots denote single trials and dashed line denotes linear fit. *Inset*, R^2 values for all sessions ($n = 25$ sessions). Open circle denotes the example session in (a). **e.** Same as (c) but for CD_{ramp} (different example session). Left and right hits are grouped (*purple*). **f.** Same as (d) but for CD_{ramp}. Same session as (e). **g.** Schematic of the randomized delay task. The delay epoch duration was randomly selected from six values (see **Methods**) with frequencies following an exponential distribution. **h.** Differences in choice selectivity and uninstructed movements between the randomized and fixed DR tasks. *Top left*, selectivity in CD_{choice} projections averaged across sessions for randomized delay (*gray*; $n = 19$ sessions) and fixed delay (*purple*; $n = 25$ sessions) tasks. Vertical lines indicate time of delay onset (*black*), go cue for the fixed delay (*purple*) and or go cue for the randomized delay (*gray*). Only trials with a delay duration of 1.2 s are shown for the randomized delay task for clarity. Gray bar at the top denotes timepoints where the slopes of the curves are significantly different ($p < 0.05$, two-sided t -test). *Bottom left*, same but for motion energy. *Top right*, time relative to delay onset that selectivity in CD_{choice} projections reaches 90% of its maximum value. Colored dots, individual sessions; black dots, outlier sessions. Asterisk denotes significant difference ($p < 0.05$, two-sided t -test) between latencies in randomized vs. fixed delay sessions. *Bottom right*, same but for session-averaged motion energy. **i.** Same as (d) for an example session of the randomized delay task. *Top*, trials with delay durations of 0.3, 0.6, 1.2, and 1.8 s are shown. *Middle and bottom*, trials with delay duration of 1.2 s only. Lines with shaded regions depict mean and 95% confidence intervals of bootstrapped distributions throughout.



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Figure 4 - Uninstructed movements are closely related to the neural encoding of context. **a.** Schematic of tasks (*top*) and context-dependent uninstructed movements. Jaw/nose/paw movements on an example trial (*middle*) and overlaid trajectories of uninstructed movements across an example session (*bottom*) for DR task (*left*) and WC task (*right*). **b.** Context decoding from high-speed video (*top*) and neural data (*bottom*) as a function of time across all sessions. Gray lines denote shuffled context labels. **c.** *Left*, heatmap of single-trial projections of neural data onto CD_{context}. *Right*, CD_{context} projections predicted from video in an example session. The chronological DR or WC block within the session is denoted by purple and orange rectangles, respectively, on the left of each plot. **d.** *Left*, trial-averaged projection of neural data onto CD_{context} and predictions from video (*dotted lines*) for the example session illustrated in (c). *Right*, scatter plot of average projection of neural data onto CD_{context} during the ITI versus average video prediction. Dots denote single trials; dashed line, line of best fit. *Inset*, R² values for all sessions (*n* = 12 sessions). Filled circle denotes the example session in (c). Lines with shaded regions depict mean and 95% confidence intervals of bootstrapped distributions throughout.

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269 Subspace decomposition of neural activity

270 We next examined whether neural signals encoding task variables could be isolated from movement-related signals, despite their correlation in time. We hypothesized that if the neural dynamics associated with cognitive and motor processes are separable, their components in the ALM should be driven by distinct latent signals.

273 Previous theoretical work demonstrated a simple mechanism that explains how neural activity can vary dynamically while ensuring that specific variables remain stably encoded⁵⁰. In this formalism, a variable of interest may be decoded from a neural population, perhaps by a downstream circuit, through a linear transformation matrix, W , which could be taken to follow from a particular pattern of synaptic connectivity. If the dimensionality of neural activity is larger than the dimensionality of the output signals decoded (i.e. if W is not square), then W will have a null space - dimensions along which neural activity can vary without affecting the decoded output⁵⁰.

279 Applying this idea to recordings from the primate motor cortex demonstrated that motor planning dynamics are confined to the null space of a linear transformation between motor cortical activity and muscle activation³⁹, thereby allowing motor planning signals to evolve dynamically in a manner that is independent of motor output. The orthogonal complement to this output-null subspace is the output-potent subspace; changes in activity along output-potent dimensions were then associated with changes in muscle activation³⁹.

284 Subsequent work identified analogous subspaces of neural activity in the primate motor cortex as the orthogonal subspaces that capture the most variance in neural activity during the delay and response epochs of a delayed-response task to capture preparatory and movement-related activity, respectively⁴⁰. This approach is effective when preparatory and movement-related dynamics are confined to distinct temporal epochs and when neural activity is exclusively related to motor preparation and motor execution, respectively, in those epochs. This approach is convenient in that it avoids the need to measure muscle activation or any other descriptor of motor output. Importantly, it also avoids the need to explicitly model the transformation between neural activity and motor output as a linear transformation. This transformation is, in general, unknown and can be highly nonlinear, particularly

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292 for movements directly controlled by central pattern generators, such as those that support much of the behavioral
293 repertoire of rodents (e.g. locomoting, breathing, whisking, licking, chewing, vocalizing, swallowing, etc.).

294 We sought to determine if this computational framework could be used to isolate the neural dynamics associated
295 with instructed and uninstructed movements from dynamics related to the encoding of choice, urgency, and context
296 in our paradigm. Following the approach of Elsayed et al.⁴⁰ we identified subspaces that maximally capture variance
297 in trial-averaged neural activity in the delay and response epochs of our DR trials (**Fig. 5a** and **Methods**). We found
298 that dynamics within ‘delay’ and ‘response’ subspaces were confined to the delay and response epochs, respectively,
299 closely resembling results observed in primates⁴⁰ (**Fig. 5b-d**). This outcome is expected when trial-averaged
300 dynamics in different epochs occupy subspaces that are largely orthogonal⁴⁰. However, activity within both
301 subspaces remained highly correlated with uninstructed movements on single trials (**Fig. 5b,e,f**), suggesting that
302 movement-related dynamics were not restricted to the ‘response’ subspace using this analytical framework. This
303 follows from the assumption that planning- and movement-related processes are strictly confined to distinct task
304 epochs, which was not the case in our paradigm. Uninstructed movements were expressed across all task epochs
305 (**Figs. 1,3, and 4**).

306 **Subspace decomposition of single-trial neural activity**

307 To avoid these limitations, we modified this analytical approach in two ways. First, because uninstructed
308 movements vary considerably from trial-to-trial, we avoided analyses of trial-averaged data and focused on single-
309 trial data. Second, rather than identifying subspaces capturing variance during the delay (when no movement is
310 assumed) and response epochs, we instead annotated all time points across a session in which animals were moving
311 and all time points at which animals were stationary. This could be straightforwardly achieved using a threshold
312 on motion energy (calculated as the magnitude of frame-by-frame changes in images captured by video). We then
313 found the orthogonal subspaces that best explained variance during all time points across a session at which animals
314 were stationary and moving (**Fig. 5h**). We termed the resulting subspaces ‘movement-null’ and ‘movement-potent’
315 subspaces. The movement-potent subspace contains dynamical patterns typically associated with movement.
316 Patterns that are observed in the absence of movements – those likely related to cognitive and other ‘internal’
317 processes – are contained within the movement-null subspace. Following this approach, we found that activity
318 within the two subspaces together explained 72% of the variance in single-trial neural activity (movement-null: 30
319 $\pm 9.5\%$, mean \pm s.d.; movement-potent: $42 \pm 8.7\%$; $n = 25$ sessions). Neural dynamics in the movement-potent
320 subspace were correlated with motion energy on single trials, as might be expected (**Fig. 5i,l,m**). Naively,
321 movement-null subspace activity might be expected to be similarly anticorrelated with motion energy because that
322 subspace is constructed to specifically capture variance during periods of animal stationarity. This outcome was
323 largely not observed. Rather, movement-null subspace activity did not display a consistent relationship with
324 movement (**Fig. 5i,l,m**) suggesting that these ‘internal’ dynamics were not only prominent in the absence of
325 movement, but persisted during movement as well, in line with the supposition that cognitive processes can persist
326 during movement.

327 Uninstructed movements were commonly observed during the delay epoch of DR trials, during motor planning, and
328 were highly correlated with putative choice and urgency signals (**Fig. 3c-h**). We examined whether the movement-
329 potent subspace might then inadvertently capture choice or urgency dynamics that are correlated in time with
330 movements. To examine this possibility, we examined movement-null and movement-potent subspaces estimated
331 using trials from the WC context only. Here, the movement-potent subspace is determined in a context in which
332 choice and urgency signals are absent²³ (**Fig. 2d** and **EDFig. 4c**), precluding the possibility that dimensions of
333 neural activity related to choice and urgency are inadvertently assigned to the movement-potent subspace due to
334 their correlation with movement. This approach yielded subspaces that were highly similar (**EDFig. 4d-f**). In
335 another control, examining movement-null and movement-potent subspaces estimated only using data recorded
336 during the response epoch of both tasks, when planning and urgency dynamics should be minimal, again yielded
337 similar results (**EDFig. 4g-i**). Finally, we estimated the movement-null subspace as the subspace defined by the top
338 principal components of activity recorded during periods of stationarity and then determined the movement-potent
339 subspace as the top principal components of dynamics not already captured in the movement-null subspace. This
340 latter procedure, which is highly conservative in avoiding the spurious assignment of internal dynamics to the
341 movement-potent subspace, again yielded similar results (**EDFig. 4j-l** and **Methods**). Together, these observations
342 suggest that the movement-potent subspace indeed captures movement-related signals, and not dynamics related to
343 internal processes that are somewhat correlated in time with movements.

344 We hypothesized that activity in the movement-null and movement-potent subspaces should capture variance in
345 neural activity across all task epochs. Animals may think and move simultaneously; thus, it follows that internal
346 dynamics contained in the movement-null space may be present during the response epoch as well. Additionally,
347 uninstructed movements occur during both the sample and delay epochs, concurrent with stimulus and choice
348 encoding. Thus, we should also observe dynamics within the movement-potent subspace during all task epochs.
349 As expected, activity within movement-null and movement-potent subspaces captured variance across epochs (**Fig.**
350 **5k**). Interestingly, the proportion of units with activity largely confined to the movement-potent subspace was larger
351 than expected by chance (**Fig. 5n** and **EDFig. 5b**; $p = 6 \times 10^{-19}$, $n = 483$ single units, see **Methods**), and larger than
352 when subspaces were identified from trial-averaged data here (**Fig. 5g**) and in non-human primates³⁹. This
353 observation suggests the identification of neuronal populations engaged solely in motor processes that could not be
354 identified without properly accounting for uninstructed movements.

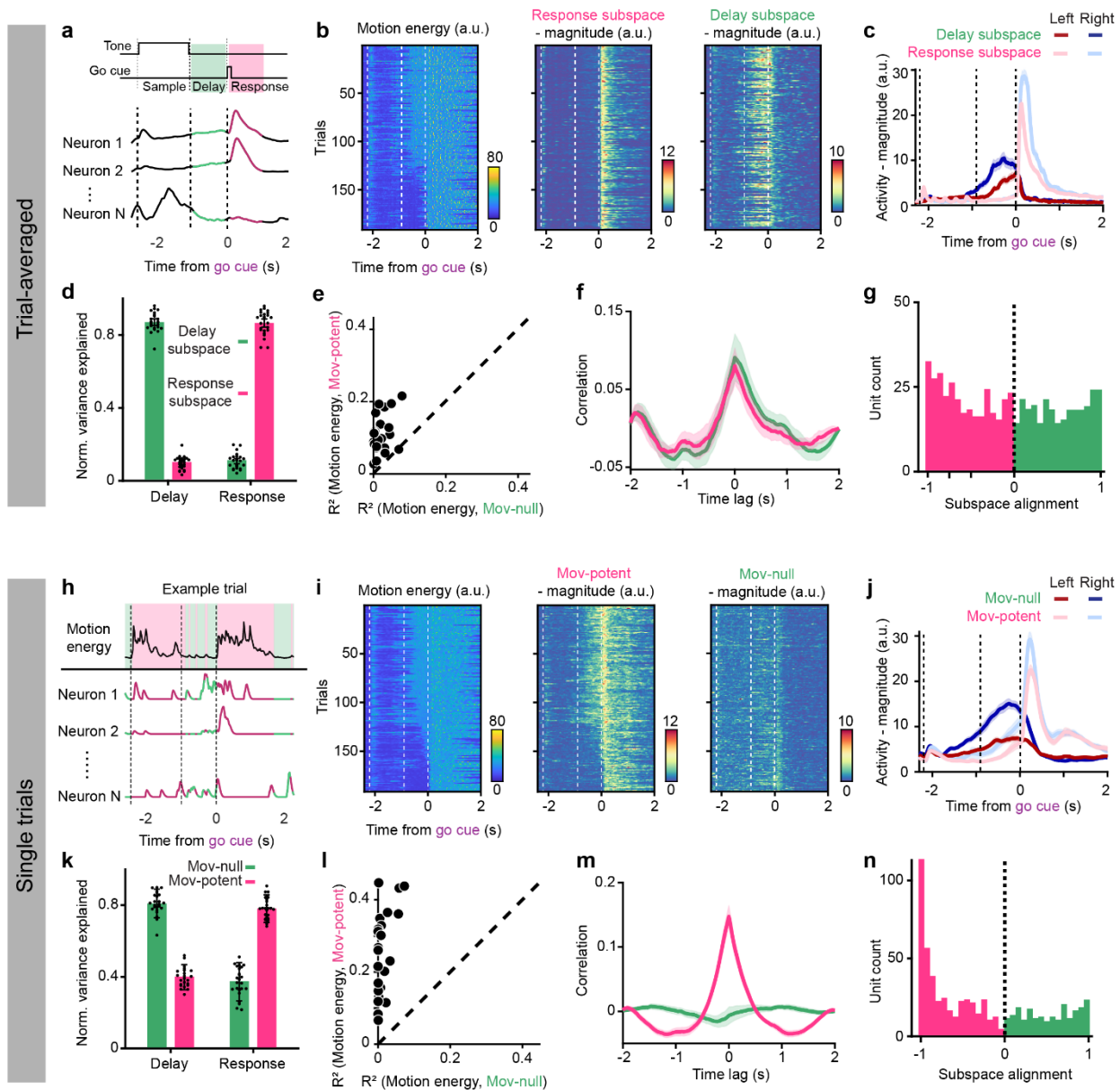
355 One of the few parameters associated with this procedure is the choice of the dimensionality of the movement-null
356 and movement-potent subspaces. We examined whether varying the dimensionality of each subspaces (from four
357 to 13) influenced these results. We found our results to be largely insensitive to subspace dimensionality (**EDFig.**
358 **6a-c**), again suggesting minimal sensitivity to choice of parameters.

359 **Internal and movement-related dynamics during motor planning**

360 The movement-potent subspace may contain at least three classes of movement-related neural dynamics: (1) motor
361 commands (and efference copies), (2) sensory feedback related to movements, and (3) internal dynamics that are
362 present *exclusively during periods of movement*. That is, if a particular internal process is “embodied,” in the sense
363 that it is mediated by the same latent dynamics as responsible for associated movements – and thus always observed
364 in the presence of those movements – then we would expect to find those latent dynamics wholly contained within
365 the movement-potent subspace (**Fig. 6c**). Dynamics supporting internal processes which are independent of
366 movements should be contained within the movement-null subspace (**Fig. 6a**). Between these extremes, we expect
367 to observe dynamics within both subspaces when a particular internal process (with associated latent dynamics in
368 the movement-null subspace) biases the expression of movements (with associated latent dynamics in the
369 movement-potent subspace) (**Fig. 6b**). In that latter case, internal processes may appear correlated with movements
370 despite being largely mediated by distinct latent dynamics.

371 To evaluate these possibilities, we examined whether putative cognitive signals (illustrated in **Fig. 2**) evolved within
372 the movement-potent and/or movement-null subspaces. We found choice selectivity – dynamics that differentiate
373 left and right DR trials – in both subspaces. The existence of choice dynamics in the movement-null subspace
374 indicates an internal representation of choice that is separable from dynamics related to the execution of choice-
375 related uninstructed movements (see **Fig. 6b**). The average time courses of choice dynamics in these subspaces
376 displayed subtle, yet notable, differences, as did their expression on error trials. Selectivity emerged quickly
377 following stimulus presentation in the movement-null subspace and did not change significantly through the delay
378 epoch (**Fig. 7a**; $p > 0.05$, paired t -test comparing selectivity during last 100ms of sample and delay epochs, $n = 25$
379 sessions **EDFig. 7c**) consistent with an internal representation driven by sensory input. On error trials, selectivity
380 in the movement-null subspace initially followed the same trajectory as correct trials but decayed following stimulus
381 offset. In the movement-potent subspace, in contrast, selectivity increased slowly during the sample epoch and
382 continued to increase monotonically during the delay epoch ($p = 3 \times 10^{-13}$, paired t -test comparing selectivity during
383 last 100ms of sample and delay epochs, $n = 25$ sessions; $p = 1 \times 10^{-5}$ comparing change in selectivity during the delay
384 epoch in movement-potent and movement-null subspaces; **EDFig. 7b**), and no significant movement-potent
385 subspace selectivity emerged on error trials. These observations suggest that sensory stimuli initially drive
386 appropriate dynamics within the movement-null subspace on error trials, but that choice is not encoded stably and
387 does not engage movement-potent dynamics related to uninstructed movements.

388 Although the trajectories of choice dynamics in each subspace shared some similarities in trial-averaged data (**Fig.**
389 **7a**), the existence of choice dynamics in both subspaces implies that they must differ markedly on single trials.
390 The onset and magnitude of activity along the component of CD_{choice} within the movement-potent subspace
391 tracked trial-type selective motion energy on a moment-by-moment basis (**Fig. 7b, c**), as expected, while there
392 was no consistent relationship between motion energy and activity along the component of CD_{choice} in the
393 movement-null subspace. Following the go cue, transient responses accompanying movement initiation were
394 absent from the movement-null subspace (**EDFig. 7a**), further suggesting the existence of choice dynamics which



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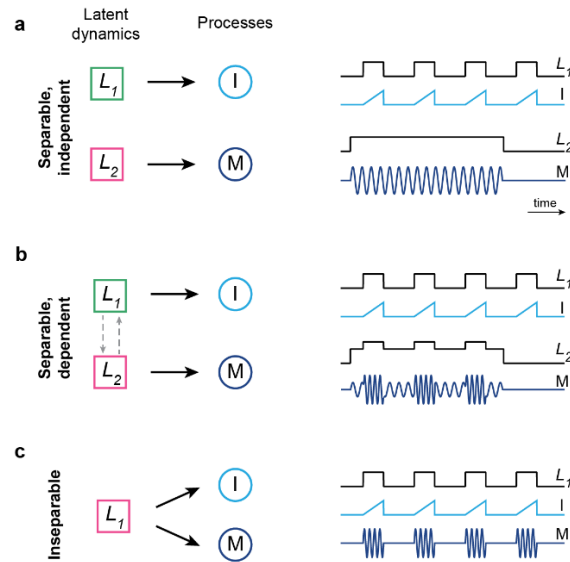
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Figure 5 – Subspace decomposition of neural activity using trial-averaged and single-trial data. **a.** Schematic of the approach for estimating delay (*green*) and response (*pink*) subspaces from trial-averaged neural data. Delay and response subspaces are determined as the orthogonal subspaces that maximally contain the variance of neural activity in the delay and response epochs, respectively. Correct trials from the DR context were used to identify subspaces. **b.** Activity during DR trials within each subspace for an example session. *Left*, motion energy across trials. *Middle*, sum-squared magnitude of activity in the response subspace. *Right*, sum-squared magnitude of activity in the delay subspace. Trials sorted by average delay epoch motion energy. **c.** Sum-squared magnitude of activity in delay and response subspaces during DR lick-left and lick-right trials for an example session. Mean and standard error across trials shown. **d.** Normalized variance explained of the neural data during DR trials by the activity in the delay and response subspaces during the delay and response epochs. Delay and response subspaces selectively capture activity in the delay and response epochs, as expected. Points indicate sessions, bar height indicates the mean across sessions, and error bars indicate standard deviation across session ($n = 25$ sessions). **e.** Variance explained (R^2) of motion energy by the sum-squared magnitude of activity in the delay and response subspaces using single-trial DR and WC data. Each point represents the mean across trials for a session ($n = 25$ sessions). **f.** Cross-correlation between motion energy and activity in the delay and response subspaces using single-trial DR and WC data. Lines indicate mean across sessions and shaded region represents standard error of the mean across sessions ($n = 25$ sessions). **g.** Subspace alignment for single units across all sessions ($n = 483$ single units, see **Methods**). Values closer to 1 indicate that more variance of a unit’s activity is contained within the preparatory subspace. **h.** Schematic of the approach for estimating movement-null and movement-potent subspaces from single-trial data. Motion energy is used to annotate when an animal is moving (*pink*) or stationary (*green*). These labels are then applied to single-trial neural data. Movement-null and movement-potent subspaces are determined as the orthogonal subspaces that maximally capture the variance of neural activity during periods of quiescence and movement, respectively. Trials from both DR and WC contexts were used to identify subspaces. **i-n.** Same as (b-f) but using the single-trial approach for estimating movement-null and movement-potent subspaces.



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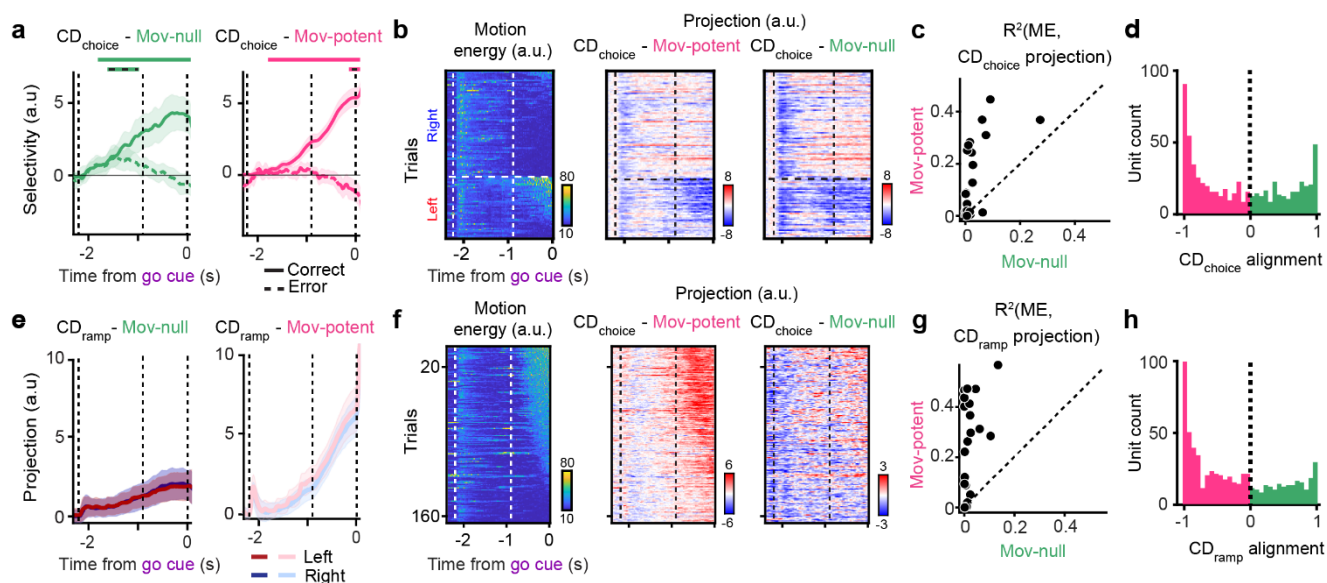
418 **Figure 6 – Schematic of potential relationships between internal and movement-related dynamics. a.** Internal and movement-related
 419 dynamics that are independent and separable. *Left*, schematic depicting an internal process (I) and a motor process (M) that are each governed
 420 by separate latent dynamics, L_1 and L_2 , respectively. L_1 and L_2 evolve within the movement-null (green) and movement-potent (pink)
 421 subspaces, respectively. *Right*, cartoon time series of separable, independent latent dynamics (L_1 and L_2) and related processes (I and M). **b.**
 422 Same as (a) in the case of latent dynamics which are separable but dependent. I and M may be loosely correlated in time. **c.** Same as (a) and

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424 are separable from ongoing movement dynamics. Importantly, we found that many single units contribute to either
 425 the movement-null or movement-potent subspace representations of CD_{choice} , but not both (**Fig. 7d** and **EDFig. 6d**),
 426 providing additional evidence of dynamics that are not only separable, but encoded by distinct populations of
 neurons (**Fig. 7d**) within the ALM microcircuit.

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428 In contrast, we found that ramping dynamics were mostly confined to the movement-potent subspace (**Fig. 7e**) –
 429 perhaps surprising given that ramping activity has been interpreted as an internal urgency or timing signal^{69–72}. This
 430 observation remained consistent when estimating movement-null and movement-potent subspaces using only WC
 431 trials or using only the response epoch of WC and DR trials (**EDFig. 8a**), when ramping dynamics were absent,
 432 confirming that ramping dynamics were not observed in the movement-potent space because of the mis-assignment
 433 of internal ramping dimensions to the movement-potent subspace because of their correlation in time with
 434 movement. We further searched for the existence of movement-null subspace ramping dynamics by explicitly
 435 identifying the dimension within the movement-null and movement-potent subspaces that maximized ramping
 436 dynamics – which could be different than the dimension that maximized ramping within the full activity space –
 437 and again failed to identify a prominent ramping signal in the movement-null subspace (**EDFig. 8b**). The relative
 438 paucity of ramping dynamics in the movement-null subspace suggests that they are not readily separable from
 associated movements in the ALM in our behavioral paradigm (see **Discussion**).



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Figure 7 – Subspace decomposition allows for the re-examination of population measures of motor planning. **a.** Selectivity (neural projections on lick-right trials minus lick-left trials) of movement-null (*left*) and movement-potent (*right*) subspace activity when projected along CD_{choice}. Mean and 5-95% CI of the bootstrap distribution for correct (solid) and error (dashed) trials shown. Horizontal bars (solid lines - correct trials; solid lines with black dashes - incorrect trials) above plot indicate when the selectivity trace is significantly different from zero ($p < 0.05$, one-sided test, bootstrap). **b.** Projections along CD_{choice} in the movement-potent subspace (*middle*), but not the movement-null subspace (*right*), follow the time-course and magnitude of motion energy (*left*) on single lick-left and lick-right trials (example session). **c.** Variance explained (R^2) of motion energy by projections along CD_{choice} in the movement-null or movement-potent subspace on single trials. Each point is the average across all trials in a session. **d.** Distribution of single unit alignment with CD_{choice} ($n = 483$ single units, see **Methods**). Distribution of movement-potent tuned units (alignment ≤ -0.8) was significantly different than expected by chance ($p = 1 \times 10^{-13}$, see **Methods**). Similarly, distribution of movement-null tuned units (alignment ≥ 0.8) was significantly different than expected by chance ($p = 7 \times 10^{-12}$). **e.** Projection of movement-null (*left*) and movement-potent (*right*) subspace activity along CD_{ramp} on lick-left and lick-right trials. Mean and 95% CI of the bootstrap distribution for correct trials shown. **f-h.** Same as (b-d) for CD_{ramp}. **h.** Distribution of single unit alignment with CD_{ramp} ($n = 483$ single units). Distribution of movement-potent tuned units (alignment ≤ -0.8) was significantly different than expected by chance ($p = 6 \times 10^{-14}$). Similarly, distribution of movement-null tuned units (alignment ≥ 0.8) was significantly different than expected by chance ($p = 1 \times 10^{-12}$).

A persistent movement-null subspace representation of context

Next, we examined projections of activity along CD_{context} in each subspace (**Fig. 8a**). We found robust contextual selectivity in both subspaces, consistent with the interpretation that the ALM contains both an internal representation of context and activity related to context-dependent movements. The transient, response-epoch dynamics observed along CD_{context} (**Fig 2d, far right**) were entirely contained within the movement-potent subspace (**Fig. 8a**) likely indicative of subtle context-specific differences in instructed movements. We then compared context selectivity (the difference in projections onto CD_{context} on DR vs. WC trials) on trials with high motion energy during the ITI ('High move' trials) and trials with little or no ITI motion energy ('Low move' trials). Context selectivity within the movement-null subspace was indistinguishable in 'High move' and 'Low move' trials. In contrast, context selectivity within the movement-potent subspace was reduced by 72% on 'Low move' trials (**Figs. 8b,c**; Full population: selectivity reduced by 0.101 ± 0.092 , mean \pm s.d., $p = 0.003$; movement-null: 0.026 ± 0.050 , $p = 0.095$; movement-potent: 0.098 ± 0.082 , $p = 1.6 \times 10^{-3}$, paired t -test; Δ selectivity between 'High move' and 'Low move' trials in movement-null vs. movement-potent: $p = 9.5 \times 10^{-3}$, paired t -test). The magnitude and timing of the reduction in movement-potent subspace context selectivity mirrored the reduction in motion energy on 'Low move' trials (**Fig. 8b, bottom**). Together, these observations demonstrate that the movement-null – but not movement-potent – subspace contains a stable representation of context that is unchanged in the presence of both instructed and uninstructed movements. Further, we found that largely distinct populations of single neurons contribute preferentially to the movement-null and movement-potent representations of context (**Fig. 8d**). These observations suggest that the analysis of context-dependent dynamics without subspace decomposition indeed spuriously conflated separate latent dynamics, encoded by different populations of neurons, likely responsible for internal

476 representations of context (contained within the movement-null subspace) and related context-dependent
477 movements (contained in the movement-potent subspace).

478 **Encoding of tongue kinematics in the movement-potent subspace**

479 Finally, we asked whether trial-type dependent activity following the go cue relates to movement, according to
480 previous suppositions^{58,6458,64} (**EDFig. 10**). Left-right selectivity along CD_{action} existed within both the movement-
481 null and movement-potent subspaces (**EDFig. 10a**), although the magnitude of selectivity in the movement-null
482 subspace was substantially smaller in magnitude. Interestingly, on error trials, activity along CD_{action} flipped to
483 resemble that of the other trial type in the movement-null subspace but flipped asymmetrically within the
484 movement-potent subspace. This asymmetry closely corresponded to an asymmetry in tongue angle, with incorrect
485 movements directed to less extreme angles when directed to the left, on average (**EDFig. 10b,c**). The component
486 of CD_{action} within the movement-potent subspace also better tracked moment-to-moment changes in tongue angle
487 during the response epoch (**EDFig. 10d,e**; $p = 2 \times 10^{-8}$, paired t -test between movement-null and movement-potent
488 variance explained of tongue angle, $n = 25$ sessions). The similarity between tongue angle, a kinematic feature, and
489 dynamics only within the movement-potent representation of CD_{action} is notable, as our analytical approach to the
490 identification of subspaces does not incorporate any kinematic information. The interpretation of action dynamics
491 within the movement-null subspace remains unclear but could relate to an internal representation of the motor plan,
492 or intention of the animal, to respond to one reward port or the other.

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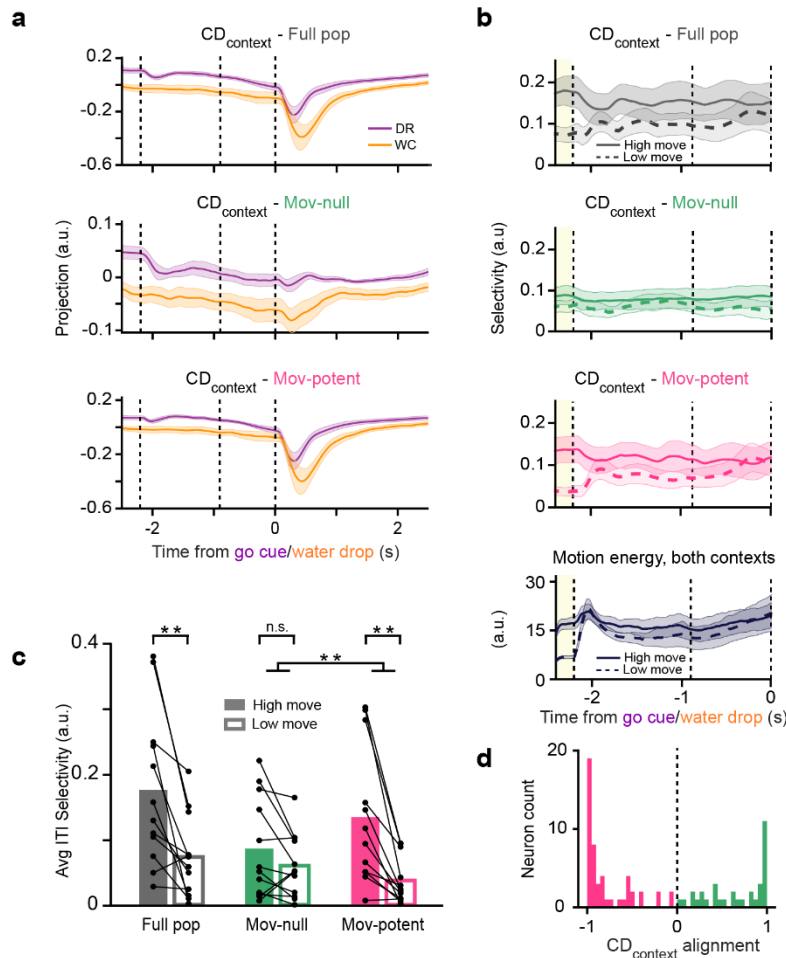
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500 **Figure 8 – A persistent, cognitive representation of context in the movement-null subspace.** **a.** Projections along CD_{context} on DR hit
501 trials (purple) and WC hit trials (orange) within the full population (top), movement-null subspace (middle), or the movement-potent
502 subspace (bottom). Solid lines denote the mean projection across sessions ($n = 12$ sessions). Note that transient response epoch dynamics are absent
503 in the movement-null subspace. **b.** Top three panels, selectivity in CD_{context} projections (DR – WC trials) on ‘high move’ (solid lines) or
504 ‘low move’ (dashed) trials. Lines denote the mean selectivity across sessions ($n = 12$) in the full space of neural activity (top), activity within
505 the movement-null subspace (second), and movement-potent subspace (third); Bottom panel, average motion energy across sessions on ‘High
506 move’ or ‘Low move’ trials. DR and WC trials are grouped together for each session. Shaded area, 95% CI across sessions. Yellow region
507 denotes ITI used to define ‘High move’ and ‘Low move’ trials. **c.** Average CD_{context} selectivity during the ITI (yellow shaded region in (b))
508 for ‘High move’ (filled bars) vs. ‘Low move’ (open bars) trials. Dots denote single sessions; bars, mean across sessions ($n = 12$ sessions).
509 Asterisks denote significant differences (**, $p < 0.01$) in CD_{context} selectivity (p -values from left to right comparing ‘High move’ vs. ‘Low
510 move’ trials, Full population: $p = 0.003$, movement-null: $p = 0.095$, movement-potent: $p = 1.6 \times 10^{-3}$; Δ selectivity between ‘High move’ and
511 ‘Low move’ trials in movement-null vs. movement-potent: $p = 9.5 \times 10^{-3}$, paired t -test). **d.** Distribution of single unit alignment with CD_{context}
512 (see **Methods**). Distribution of movement-potent tuned units (alignment ≤ -0.8) was significantly different than expected by chance ($p =$
513 2×10^{-8} , see **Methods**). Similarly, distribution of movement-null tuned units (alignment ≥ 0.8) was significantly different than expected by
514 chance ($p = 9 \times 10^{-6}$, $n = 84$ single units). Lines with shaded regions depict mean and 95% confidence intervals across sessions throughout.

515 **Discussion**

516 We aimed to understand whether the neural correlates of three cognitive variables commonly examined in
517 sensorimotor decision-making tasks – choice, urgency, and context – were separable from the neural encoding of
518 related uninstructed movements in the mouse ALM. We addressed this question by adapting an analytical formalism
519 in which neural activity is decomposed into orthogonal subspaces – here, a movement-potent subspace containing
520 dynamics related to the execution of movements and a complementary movement-null subspace containing
521 dynamics related to cognitive and other internal processes^{39,40,50}. Extending upon this framework allowed us to
522 consider single-trial neural data recorded in the presence of uninstructed movements that can vary dramatically
523 across trials in their timing and identity (**Fig. 5**).

524 **Separability of choice, urgency, and context encoding from movement-dynamics**

525 Using this approach, we demonstrated that the ALM contains neural dynamics related to encoding of choice and
526 context that could be readily separated from movements, despite both cognitive variables being strongly correlated
527 with movements in time (**Fig. 7** and **Fig. 8**). Choice-selective signals were present in both movement-null and
528 movement-potent subspaces (**Fig. 7a**), consistent with the interpretation that a cognitive representation of choice
529 within the movement-null subspace biases the probability and identity of uninstructed movements in a choice-
530 selective manner. Supporting this interpretation, movement-null and movement-potent subspace dynamics followed
531 similar trajectories, on average, but differed on single trials (**Fig. 7b**). Further, movement-null subspace encoding
532 of choice exhibited features absent from encoding within the movement-potent subspace. Choice encoding
533 increased in the presence of external stimuli, while movement-potent subspace encoding continued to increase
534 monotonically after sensory stimuli were removed, mirroring the temporal evolution of animal's uninstructed
535 movements. On error trials, stimulus-driven choice encoding initially evolved correctly – but only within the
536 movement-null subspace – before decaying prior to the go cue (**Fig. 7a**). Together, these results suggest choice-
537 related cognitive and motor processes that are governed by separable latent dynamics (**Fig. 6b**).

538 Context was stably encoded within the movement-null subspace during all trial epochs and the inter-trial interval
539 (**Fig. 8a-c**). Although context was strongly represented in the movement-potent subspace as well, these dynamics
540 were significantly reduced in the absence of movement and were also modulated by animals' instructed movements.
541 These results suggest a persistent internal representation of context in the movement-null subspace in addition to
542 distinct movement-potent-subspace dynamics related to context-dependent movements, again indicative of related,
543 but separable, latent dynamics (**Fig. 6b**).

544 Surprisingly, ramping dynamics proposed to underlie urgency (or timing)^{69–72} were principally represented in the
545 movement-potent subspace (**Fig. 7e**) indicating the possible absence of an internal representation of urgency that
546 can be dissociated from movements in the ALM. Although it remains possible that a separable representation of
547 urgency exists elsewhere in the brain, our results could alternatively imply that urgency is typically embodied, or
548 inseparable from movement, in our behavioral paradigm^{74,75}.

549 In contrast to these cognitive variables, encoding of kinematic features of movements, which were not used to
550 determine subspaces, were confined to the movement-potent subspace (**EDFig. 10**), consistent with our
551 interpretation of these subspaces.

552 **Subspace decomposition**

553 The approach to subspace decomposition presented here represents a means for assessing the issue of separability,
554 and for isolating separable dynamics into movement-related and internal components for further analyses across a
555 wide range of experimental preparations. This method only requires annotation of when animals are moving and
556 utilizes a robust analytical approach that does not require fine-tuning of parameters.

557 A number of alternative methods have been proposed to evaluate neural dynamics associated with cognitive
558 processes in the presence of movement. The most common approach, which assumes separability of cognitive and
559 motor dynamics, is to parameterize movements as fully as possible and 'regress them out.' However,
560 parameterization of movement, particularly the orofacial and postural movements that have been associated with
561 strong, brain-wide neural dynamics^{30,31,76}, can be challenging. Further, this approach typically assumes a linear
562 relationship between neural activity and kinematic (or electromyographic) variables – an assumption unlikely to
563 hold for common movements mediated by central pattern generators and other highly nonlinear mechanisms^{77–79}.
564 Subspace decomposition is straightforward to implement under a range of experimental conditions and is entirely
565 consistent with complex, nonlinear relationships between neural activity and movement variables, as expected for

566 many orofacial movements⁷⁷ and locomotion. Methods for properly interpreting cognitive signals in the presence
567 of related movements on single trials will be vital for increasingly common experimental paradigms examining
568 freely moving animals performing complex, naturalistic behaviors⁸⁰⁻⁹⁰.

569 Determination of movement-null and movement-potent subspaces as the orthogonal subspaces containing the most
570 variance in neural activity during periods of stationarity and movement is conservative in the assignment of
571 dynamics to the movement-null subspace. It is more likely that dynamics associated with cognitive and other
572 internal processes are misassigned to the movement-potent subspace than vice-versa. For example, dynamics
573 associated with “embodied” cognitive processes that always occur during periods of movement will only be
574 represented in the movement-potent subspace (**Fig. 6c**). Thus, the dynamics within the movement-null subspace are
575 highly likely to indicate signals related to internal processes. Straightforward variations of this approach can be
576 used to determine subspaces in a manner that is more conservative in assigning dynamics to the movement-potent
577 subspace – for example, estimating subspaces from response epoch data (‘instructed’ movements), from WC trials
578 (where uninstructed movements occur in the absence of choice and urgency signals) or simply through principal
579 component decomposition of activity recorded during periods of stationarity (**EDFig. 4j-l**). Nevertheless, the
580 similarity of results obtained using these analytical variations argue against the possibility that cognitive dynamics
581 associated with choice and urgency were inadvertently assigned to the movement-potent subspace, due to their
582 correlation in time with uninstructed movements, in this study.

583 That many individual units contribute solely to one subspace (**Figs. 5n, 7d,h, 8d**) suggests that the complementary
584 subspaces we identify could map to distinct cell types within the underlying cortical circuit^{63,91}. The suggestion that
585 individual neurons only appear to code for either internal or movement-related variables when uninstructed
586 movements are accounted for (**Figs. 5n, 7d,h, 8d**) underscores the importance of properly considering movements
587 in future work focused on the roles of functionally, anatomically, and/or transcriptomically-defined cell-types in
588 neural computation.

589 Our approach to subspace decomposition makes several simplifying assumptions. First, movements of the posterior
590 torso, hindlimbs, or tail of the animal were not routinely captured via videography. It remains possible, albeit
591 unlikely, that animals routinely perform movements confined to these portions of the body without concomitant
592 movement of the forepaws, head, neck, face, or whiskers²⁶. Periods of stationarity were no doubt algorithmically
593 classified imperfectly and could have contained subtle movements below our threshold for detection. Second, we
594 did not consider potential time lags between motion energy captured via videography and the dynamics associated
595 with motor and/or sensory signals⁷³. However, these time lags, on the order of a few tens of milliseconds, should
596 be much shorter than the timescale of dynamics explored in this study. Third, the set of signals related to movement
597 and/or cognitive processes may also be better described as occupying nonlinear manifolds rather than linear
598 subspaces^{92,93}. Subspaces (or manifolds) could also shift dynamically during behavior following changes in the
599 activation of upstream or downstream brain regions^{94,95} as a result of changes in context^{16,48,96}. Considering this
600 additional complexity may improve estimates of the dynamics associated with specific neural processes.

601 **Variable relationships between cognition and movement**

602 The dynamics associated with some cognitive processes and movements may be largely independent (**Fig. 6a**) –
603 perhaps in the case of the locomotor patterns of an individual walking down the street while thinking about what
604 they will cook for dinner. On the other hand, some cognitive processes may be embodied, in the sense that they are
605 tightly linked to externally observable changes in the body (**Fig. 6c**), such as the relationship between arousal and
606 changes in pupil diameter⁹⁷⁻⁹⁹. Between these extremes may be movements which are correlated with - but mediated
607 by neural dynamics that are separable from - those supporting cognitive and other internal processes. The probability
608 and identity of uninstructed movements in this study appeared related to choice and context (**Fig. 6b**), but with a
609 high degree of trial-to-trial and moment-to-moment variability unlikely to reflect commensurate variability in the
610 cognitive processes to which they relate. Correlations between cognitive processes and movements may also differ
611 considerably in trained, head-fixed animals compared to naturalistic settings^{83,88}. This high degree of variability in
612 these relationships underscores the importance of developing and utilizing tools for assessing whether the neural
613 activity supporting cognitive processes can be dissociated from those related to movements in particular
614 experimental paradigms of interest.

615 The tight link between cognition and movement might suggest that some cognition-associated movements may be
616 beneficial for behavior. For example, postural adjustments may be highly related to decisions or motor plans,

617 enabling faster reaction times and/or more accurate movements^{76,100}. Movements are also essential for some internal
618 processes – those supporting active sensation of the environment surely facilitate the construction and continual
619 updating of internal models of the environment^{30,46}. However, just as separability may not be consistent across
620 movements and cognitive processes, not all cognition-associated movements may have a functional role^{30,101}. A
621 poker player’s ‘tell’ may be highly related to their cognitive state, yet may not directly aid the player in the game.
622 Regardless of their functional relationship, understanding the separability of cognitive processes and associated
623 movements in a wide variety of experimental settings is essential for the interpretation of neural dynamics observed
624 during behavior.

625 **Methods**

626 Animals

627 This study used data collected from 17 mice; both male and female animals older than 8 weeks were used. Six
628 animals were used for the two-context task and were either C57BL/6J (JAX 000664) or VGAT-ChR2-EYFP (-/-).
629 An additional three animals, either C57BL/6J or VGAT-ChR2-EYFP (-/-) were trained only on the delayed response
630 task. A separate cohort of four animals were used in the randomized delay task (VGAT-ChR2-EYFP +/-) or
631 VGAT-ChR2-EYFP (-/-). Finally, four VGAT-ChR2-EYFP (+/-) animals were used in optogenetics experiments.
632 Mice were housed in a 12-hour reverse dark/light cycle room with ad libitum access to food. Access to water was
633 restricted during behavioral and electrophysiology experiments (see *Mouse behavior*). Sample sizes were not
634 determined using any statistical tests.

636 Surgical procedures

637 All surgical procedures were performed in accordance with protocols approved by the Boston University
638 Institutional Animal Care and Use Committee. For post-operative analgesia, mice were given ketoprofen (0.1 mL
639 of 1 mg/mL solution) and buprenorphine (0.06 mL of 0.03 mg/mL solution) prior to the start of all surgical
640 procedures. Mice were anesthetized with 1-2% isoflurane and placed on a heating pad in a stereotaxic apparatus.
641 Artificial tears (Akorn Sodium Chloride 5% Ophthalmic Ointment) were applied to their eyes and a local anesthetic
642 was injected under the skin (Bupivacaine; 0.1 mL of 5 mg/mL solution) above the skull. The skin overlying the
643 skull was removed to expose the ALM (AP: +2.5 mm, ML: +1.5 mm), bregma, and lambda. The periosteum was
644 removed and the skin was secured to the skull with cyanoacrylate (Krazy Glue) around the margins. For
645 electrophysiology experiments, a headbar was implanted just posterior to bregma and secured with superglue and
646 dental cement (Jet™). Wells to hold cortex buffer (NaCl 125mM, KCl 5mM, Glucose 10mM, HEPES 10mM,
647 CaCl₂ 2mM, MgSO₄ 2mM, pH 7.4) during electrophysiology recordings were sculpted using dental cement and a
648 thin layer of superglue was applied over any exposed bone.

649
650 For optogenetics experiments, after headbar implantation, bone overlying frontal cortex was thinned bilaterally with
651 a dental drill and removed, exposing the frontal cortex. A glass window was then implanted over each hemisphere
652 and secured to the skull with cyanoacrylate¹⁰². Before performing photoinactivation experiments, any bone regrowth
653 was removed.

655 Mouse behavior

656 Following surgery, mice were allowed to recover for ~1 week and then water restricted, receiving 1.0 mL of water
657 per day. Behavioral training commenced after animals had been water restricted for 3-4 days. If animals received
658 less than 1.0 mL during training, they were supplemented with additional water.

659 All mice used in experiments were first trained on the delayed-response task with a fixed delay epoch until they
660 reached at least 70% accuracy. At the beginning of each trial, one of two auditory tones lasting 1.3 s were played;
661 the tone indicating a ‘right’ trial was white noise while the tone indicating a ‘left’ trial was a pure tone (8 kHz
662 pulses). The delay epoch (0.9 s for 12 mice, 0.7 s for 1 mouse and linearly time warped to 0.9 s) started after the
663 completion of the sample tone. Following the delay epoch, an auditory go cue was played (swept-frequency cosine
664 [chirp], 10 ms) after which animals were rewarded with ~3 μL of water for contacting the correct lickport. Lickport
665 contacts before the response epoch resulted in the current task epoch restarting, ensuring that they could not progress
666 to the next task epoch until they had stopped licking for the specified length of the current epoch. If the animal did
667 not respond within 3 s of the go cue, this was considered an ‘ignore’ trial, although responses were typically
668 registered within 300 ms of the go cue.

669 Mice used for the two-context task (**Figs. 1,2,4,8** and **EDFig. 1-3**) were introduced to the water-cued context after
670 they were fully trained on the delayed-response context and at least two days before the first electrophysiology
671 recording session. A behavioral session began with ~100 DR trials and was then followed with alternating blocks
672 of WC and DR trials. Each interleaved block was 10-25 trials, with no fixed block duration. All sessions started
673 with DR trials. Pilot sessions beginning with WC trials had to be terminated early due to a high ‘no response’ rate,
674 likely due to the mouse becoming sated early in the session. In a WC trial, all auditory cues were omitted and a ~3
675 μ L water reward was presented randomly from either lickport. Trials in which the animal contacted the lickport
676 prior to the reward (‘early lick’) were omitted from analyses. Inter-trial intervals were randomly drawn from an
677 exponential distribution with mean 1.5 s. There were no explicit cues during the ITI to indicate to the animal which
678 context block it was in.

679 For the randomized delay task (**Fig. 3g-h**), mice were first fully trained on the fixed delay DR task (delay duration
680 of 0.9 s). The delay epoch length was then randomized – the duration was randomly selected from six possible
681 values (0.3, 0.6, 1.2, 1.8, 2.4, and 3.6 s). The probability of each delay duration being selected was assigned such
682 that it resembled a probability density function of an exponential distribution with $\tau = 0.9$ s, as in ref⁶⁵. Animals
683 were trained on this version of the task until they became experts (> 70% accuracy and < 20% early lick rate).
684

685 Videography analysis

686 High-speed video was captured (400 Hz frame rate) from two cameras (FLIR, Blackfly® monochrome camera,
687 Model number: BFS-U3-16S2M-CS). One provided a side view of the mouse and the other provided a bottom view.
688 We tracked the movements of specific body features using DeepLabCut⁵² (**Figs. 1,3,4**). The tongue, jaw, and nose
689 were tracked using both cameras while the paws were only tracked using the bottom view. Position and velocity of
690 each tracked feature was calculated from each camera. The x and y position of each kinematic feature was extracted
691 from the output of DeepLabCut. Missing values were filled in with the nearest available value for all features except
692 for the tongue. The velocity of each feature was then calculated as the first-order derivative of the position vector.
693 Tongue angle and length were found using the bottom camera. Tongue angle was defined as the angle between the
694 vector pointing from the jaw to the tip of the tongue and the vector defining the direction the mouse was facing.
695 Tongue length was calculated as the Euclidean distance from the jaw to the tip of the tongue.

696 Plots of kinematic feature overlays (**Figs. 1e, 3a, 4a** and **EDFig. 3**) were generated by plotting an [r, g, b] value for
697 each timepoint, t , where the values were specified by [KinFeature1_t, KinFeature2_t, KinFeature3_t]. All kinematic
698 features (speed or motion energy) were first standardized by taking the 99th percentile across time and trials and
699 normalizing to this value.
700

701 Motion energy

702 The motion energy for a given frame and pixel was defined as the absolute value of the difference between the
703 median value of the pixel across the next 5 frames (12.5 ms) and the median value of the pixel across the previous
704 5 frames (12.5 ms). Motion energy for each frame was then converted to a single value by taking the 99th percentile
705 (~700 pixels) of motion energy values across the frame. Motion energy calculated in this manner was high during
706 overt movements over small regions of pixel space, such as during whisking, while remaining relatively low during
707 passive respiration that corresponded to subtle motion across the animal’s body. A threshold above which an animal
708 was classed as moving, was defined on a per session basis manually. Motion energy distributions, per session, were
709 bimodal, showing a large peak with little variance at low motion energy values and a second, smaller peak, with
710 high variance at large values. The threshold was set as the motion energy value separating these two modes. We
711 found that this method of setting the threshold captured both short and long duration movements. Alternative
712 methods, such as defining a baseline period of no movement against which to compare, were less successful due to
713 the variability in timing of the movements across trials.
714

715 Photoinactivation experiments

716 Optogenetic photoinactivation was deployed on ~30% of trials selected at random. A ‘masking flash’ (470 nm
717 LED’s LUXEON REBEL LED) controlled by an Arduino Teensy microcontroller (100 ms pulses, at 10 Hz) was
718 delivered constantly for the duration of the session to prevent mice from differentiating control and
719 photoinactivation trials. A 488-nm laser (Coherent OBIS 488 nm LX 150 mW Laser System) was used for all
720 photoinactivation experiments. ChR2-assisted photoinactivation (**Fig. 1b,c,g-** and **EDFig. 1b-d**) was performed
721 through a cranial window¹⁰² (see **Surgical Procedures**), which replaced bone over the frontal cortex. Light was

722 delivered either at the start of the delay epoch, or at the start of the response epoch (only one epoch tested per
723 session). A power density of 1.5 mW/mm² was used for all photoinactivation experiments.

724 For delay epoch photoinactivation (**Fig. 1g-i** and **EDFig. 1b**), light was delivered at the onset of the delay epoch
725 and lasted for 0.6 s followed by a 0.2 s linear ramp down. We targeted one of three regions per session: bilateral
726 motor cortex (ALM and tjM1), bilateral ALM, or bilateral tjM1. A scanning galvo system (THORLABS GPS011)
727 was used to simultaneously target both hemispheres by scanning at 40 Hz. The beam (2 mm diameter) was centered
728 around the following locations: ALM (AP 2.5 mm, ML 1.5 mm), tjM1 (AP 1.75 mm, ML 2.25 mm), motor cortex
729 (i.e. ALM and tjM1; AP 2.25 mm, ML 1.85 mm). Due to their proximity, when specifically targeting ALM or tjM1,
730 Kwik-Cast™ (World Precision Instruments) was applied to the surrounding regions to prevent photoinactivation of
731 other regions. For photoinactivation at the go cue (**Fig. 1b,c** and **EDFig. 1c,d**), light was delivered to the motor
732 cortex for 0.8 s followed by a 0.2 s ramp down beginning at the go cue presentation.

733 Electrophysiology recordings

734 Extracellular recordings were performed in the ALM using one of two types of silicon probes: H2 probes, which
735 have two shanks, each with 32 channels with 25- μ m spacing (Cambridge Neurotech) or Neuropixels 1.0¹⁰³ which
736 have one shank and allow recording from 384 channels arranged in a checkerboard pattern (IMEC). For recordings
737 with H2 probes, the 64-channel voltage signals were multiplexed using a Whisper recording system (Neural
738 Circuits, LLC), recorded on a PXI-8133 board (National Instruments) and digitized at 14 bits. The signals were
739 demultiplexed into 64 voltage traces sampled at 25 kHz and stored for offline analysis.

740 At least 6 hours before recording, a small craniotomy (1-1.5 mm diameter) was made over ALM (AP 2.5 mm, ML
741 1.5 mm). 2-5 recordings were performed on a single craniotomy on consecutive days. After inserting the probes
742 between 900 and 1100 μ m (MPM System, New Scale Technologies), brain tissue was allowed to settle for at least
743 5 minutes before starting recordings. All recordings were made using SpikeGLX
744 (<https://github.com/billkarsh/SpikeGLX>).

745 Behavioral analysis

746 All sessions used for behavioral analysis had at least 40 correct DR trials for each direction (left or right) and 20
747 correct WC trials for each direction, excluding early lick and ignore trials, which were omitted from all analyses.
748 To assess the impact of ALM photoinactivation on movement initiation, we first calculated the percent of trials with
749 a correct lick within 600 ms of the go cue/water drop (**Fig. 1c**). To find the fraction of time with the tongue visible
750 during the photoinactivation period (**EDFig. 1d**), for each trial we found the number of time-points within the 1 s
751 after the go cue/water drop where the tongue was labelled as visible by DeepLabCut and divided that by the total
752 number of time-points within the photoinactivation period. This was then averaged for all control or
753 photoinactivation trials for a given session.

754 To assess the impact of bilateral MC/ALM/tjM1 photoinactivation during the delay epoch, the average motion
755 energy during the delay epoch was calculated separately for right and left control vs. photoinactivation trials (**Fig.**
756 **1h** and **EDFig. 1b**).

757 Electrophysiology recording analysis

758 JRCLUST¹⁰⁴ (<https://github.com/JaneliaSciComp/JRCLUST>) and/or Kilosort3¹⁰⁵
759 (<https://github.com/MouseLand/Kilosort>) with manual curation using Phy (<https://github.com/cortex-lab/phy>) were
760 used for spike sorting. A unit was considered a well-isolated single unit based on manual inspection of its ISI
761 histogram, separation from other units, and its stationarity across the session¹⁰⁶. Units that passed manual curation
762 but had a higher ISI violation rate were called multiunits. Recording sessions were only included for analysis if
763 they had at least 10 units (see **EDFig. 2** for a distribution of neuron counts across sessions). For the DR task, we
764 recorded 1651 units (483 single units) in ALM from 25 sessions using 9 mice. In 12 sessions from 6 mice, animals
765 performed the two-context task. 522 units (214 well-isolated single units) were recorded in these sessions. Finally,
766 for the randomized delay task, we recorded 845 units (288 well-isolated single units) in ALM from 19 sessions
767 using 4 mice. For subspace alignment (**Figs. 5g,n, 7d,h**, and **Fig. 8d**) and single-unit selectivity analyses (**Fig. 3g**
768 and **EDFig. 4c**) only well-isolated single units with firing rates exceeding 1 Hz were included. All units with firing
769 rates exceeding 1 Hz were included in all other analyses.

770 To find choice-selective neurons, forty trials were subsampled for both right and left correct trials and a *ranksum*
771 test was used to compare spike counts for each unit during the sample, delay, or response epochs. Selective units

772 were those with significantly different spike counts ($p < 0.05$) during a given epoch. Context-selective units were
773 defined in a two-step process to ensure that we were not conflating context selectivity with slow changes in animal
774 engagement/motivation over each session. First, forty trials each were subsampled for DR and WC trials and spike
775 counts were compared ($p < 0.05$, *ranksum* test) during the ITI (the 300 ms preceding the sample tone onset) when
776 the animal received no external cues to indicate which context it was in. Because sessions always began with a DR
777 block and often ended with a WC block, it is possible that differences in firing rates across contexts defined in this
778 way could be representing time within the session. To account for this, for each unit identified in the first step, we
779 calculated the difference in spike rate for each pair of DR and WC blocks (e.g. a session with five blocks, DR-WC-
780 DR-WC-DR, would have nPairs=4 adjacent, overlapping block pairs) and included units as context-selective only
781 if their *preferred* context (context with a higher spike rate) was the same for at least nPairs - 1 of the block pairs.

782 Selectivity in the neural population (**EDFig. 4c**) was calculated as the difference in spike rate on *preferred* – *non-*
783 *preferred* trials in choice-selective units, with *preferred* trials referring to the trial type with a higher spike rate for
784 each unit.

785 Coding direction analysis

786 Coding directions (CD) were defined as directions in neural activity state space, defined by firing rates, that
787 maximally separated trajectories of two conditions.

788 CD_{choice} and CD_{action} were calculated as:

$$789 \quad \mathbf{v} = \frac{\bar{\mathbf{x}}_{lickright} - \bar{\mathbf{x}}_{lickleft}}{\sqrt{\text{var}(\mathbf{x}_{lickright}) + \text{var}(\mathbf{x}_{lickleft})}}$$

$$791 \quad \mathbf{CD} = \frac{\mathbf{v}}{\sum |\mathbf{v}|}$$

792 For each unit, the mean spike rate difference between right lick trials, $\bar{\mathbf{x}}_{lickright}$, and left lick trials, $\bar{\mathbf{x}}_{lickleft}$, was
793 calculated in a 400 ms time interval. $\bar{\mathbf{x}}_{lickright}$ and $\bar{\mathbf{x}}_{lickleft}$ were then individually baseline subtracted and scaled
794 by baseline standard deviation before calculating CDs (baseline: -2.4 to -2.2 seconds relative to the go cue, during
795 the ITI). CD_{choice} was calculated in the last 400 ms of the delay epoch and CD_{action} was calculated in the first 400
796 ms of the response epoch. The vector \mathbf{v} was then obtained by normalizing by the square root of the sum of the
797 variances across conditions. Finally, \mathbf{v} was normalized by its L₁ norm to ensure projections do not scale with the
798 length of \mathbf{v} , the number of units simultaneously recorded.

801 CD_{ramp} was calculated as:

$$802 \quad \mathbf{v} = \frac{\bar{\mathbf{x}}_{delay} - \bar{\mathbf{x}}_{ITI}}{\sqrt{\text{var}(\mathbf{x}_{delay}) + \text{var}(\mathbf{x}_{ITI})}}$$

$$804 \quad \mathbf{CD} = \frac{\mathbf{v}}{\sum |\mathbf{v}|}$$

805 This calculation was similar to the calculations of CD_{choice} and CD_{action} but incorporated data from all correct DR
806 trials during the last 400 ms of the delay epoch, $\bar{\mathbf{x}}_{delay}$, and during the ITI (300 ms preceding the sample tone
807 onset), $\bar{\mathbf{x}}_{ITI}$. $\bar{\mathbf{x}}_{ITI}$, $\bar{\mathbf{x}}_{delay}$ and $\bar{\mathbf{x}}_{ITI}$ were both standardized using the baseline statistics from all correct DR trials.

810 To find CD_{context}, we first calculated a CD_{context}^{*p*} for each pair, *p*, of DR and WC blocks in a session. If the session
811 ended with a WC block, that block was excluded. CD_{context}^{*p*} was calculated as:

$$812 \quad \mathbf{v}_p = \frac{\bar{\mathbf{x}}_{DR^p} - \bar{\mathbf{x}}_{WC^p}}{\sqrt{\text{var}(\mathbf{x}_{DR^p}) + \text{var}(\mathbf{x}_{WC^p})}}$$

$$813$$

814

815

$$\mathbf{CD}_p = \frac{v_p}{\sum |v_p|}$$

816

817

818 $\mathbf{CD}_{\text{context}}$ was then defined as the average over all $\mathbf{CD}_{\text{context}}^p$ in a session. The calculation of $\mathbf{CD}_{\text{context}}^p$ was similar
819 to the calculation of other CDs but incorporated data from the ITI of correct DR, \bar{x}_{DR^p} , and correct WC, \bar{x}_{WC^p} ,
820 trials in a given pair of blocks. \bar{x}_{DR^p} and \bar{x}_{WC^p} were standardized using the baseline statistics from all correct DR
821 and WC trials.

822 $\mathbf{CD}_{\text{action}}$ was orthogonalized to $\mathbf{CD}_{\text{choice}}$ to exclusively capture response epoch selectivity that emerges after the go
823 cue. $\mathbf{CD}_{\text{ramp}}$ was orthogonalized to $\mathbf{CD}_{\text{action}}$ and $\mathbf{CD}_{\text{choice}}$ to remove selectivity that may emerge during the response
824 epoch that is also captured in $\mathbf{CD}_{\text{action}}$. Orthogonalization was performed using the Gram-Schmidt process.

825 Projections of the population activity, $\mathbf{x} \in \mathbb{R}^{(B \cdot K) \times N}$ along the CD were calculated as:

826

827

$$\text{proj} = \mathbf{CD}^T * \mathbf{x}$$

828

829 where B is the number of time bins, K the number of trials, N the number of neurons, and T is the transpose operator.

830 For the randomized delay task, trials with non-1.2 s delay lengths were used to calculate $\mathbf{CD}_{\text{choice}}$ (fit trials), always
831 using the last 600 ms of the delay epoch as the time interval for calculation⁶⁵. Population activity from trials with
832 1.2 s delays (test trials) were then projected along the $\mathbf{CD}_{\text{choice}}$ (**Fig. 3h**, *top left* and **Fig. 3i**, *middle*). For
833 visualization purposes, trials with all delay lengths (including fit trials) were projected along $\mathbf{CD}_{\text{choice}}$ in **Fig. 3i**,
834 *top*.

835 Reliability of choice decoding from $\mathbf{CD}_{\text{choice}}$

836 An ROC-AUC analysis was performed to estimate the reliability of choice decoding from projections along $\mathbf{CD}_{\text{choice}}$
837 on a single session basis (**EDFig. 2c**). For each session, equal numbers of correct left and right lick trials were split
838 into a training (70%) and testing set (30%). $\mathbf{CD}_{\text{choice}}$ was calculated from the activity of the neural population using
839 training trials as described above. Activity from testing trials was projected along $\mathbf{CD}_{\text{choice}}$ and provided as input to
840 a logistic regression model (fitglm() in MATLAB with distribution='Binomial', link='logit'). The model was
841 optimized to predict the animal's choice on a particular trial from the delay epoch $\mathbf{CD}_{\text{choice}}$ activity. The model
842 output was then passed into MATLAB's perfcurve() function to obtain a receiver operating curve (ROC). Reliability
843 of decoding was measured as the area under the ROC (AUC), shown in the inset of **EDFig. 2c**.

844

845 Choice/context decoding from neural population or kinematic features

846 We trained logistic regression models to predict either animal choice (**Fig. 3b**) or behavioral context (**Fig. 4b**) from
847 either kinematic features or single trial neural activity. The kinematic regressors were made up of the x and y
848 positions and velocities of DeepLabCut-tracked features (tongue, jaw, and nose), as well as the tongue length, angle,
849 and motion energy. The neural regressors were the firing rates of the units simultaneously recorded within each
850 session. Equal numbers of correct left and right lick trials were used for this analysis. A separate model was trained
851 at each time bin for both neural and kinematic decoding. Models were trained with ridge regularization and 4-fold
852 cross-validation with 30% of trials held out for testing. Chance accuracy was obtained by shuffling choice/context
853 labels across trials. Accuracy of the prediction was defined as:

854

855

$$\text{Accuracy} = \frac{\text{Number of correct predictions}}{\text{Total number of predictions}}$$

856

857 Emergence of $\mathbf{CD}_{\text{choice}}$ selectivity/motion energy in randomized vs. fixed delay tasks

858 To find selectivity within the $\mathbf{CD}_{\text{choice}}$ projection (**Fig. 3h**, *top left*) we found the difference between the trial-
859 averaged projection on right and left trials for each session. We then found the maximum selectivity value prior to
860 the go cue and identified the first time point, relative to delay onset, for the selectivity trace to exceed 90% of the

861 maximum value (**Fig. 3h, top right**). The same metric was found using session-averaged motion energy in **Fig. 3h,**
 862 *bottom panels*.

863
 864 Predicting projections along coding directions from kinematic features

865 We trained support vector machines (SVMs) to predict projections along CD_{choice}, CD_{ramp}, and CD_{context}. Correct
 866 DR trials were used for predicting CD_{choice} and CD_{ramp} projections; correct DR and WC trials were used for
 867 predicting CD_{context}. For predicting CD_{context}, the regressors were made up of the x and y positions and velocities
 868 of DeepLabCut-tracked features (multiple points on the tongue, jaw, and nose taken from two camera angles), as
 869 well as the tongue length, angle, and motion energy (totaling 60 regressors). Only the sample and delay epoch were
 870 considered when predicting CD_{choice} and CD_{ramp} projections; because of this, any tongue-related metrics were not
 871 included as regressors in these analyses (totaling 55 regressors). Projections and kinematic features were first mean-
 872 centered and scaled to unit variance before input to the regression model. The previous B time bins of kinematic
 873 data were used to predict the current bin's neural data (B=6, each bin is 5 ms). Models were trained with ridge
 874 regularization and 4-fold cross-validation. The models were tested on held-out testing data (40% of trials for
 875 CD_{choice} and CD_{ramp}; tested on 30% of trials for CD_{context}). To assess the prediction quality between projections and
 876 model predictions, we calculated the variance explained as:

877
 878
$$R^2 = 1 - \frac{\sum_t (y_t - \hat{y}_t)^2}{\sum_t (y_t - \bar{y})^2}$$

879 where y_t is the value of the projection at time t , \hat{y}_t is the prediction, and \bar{y} is the mean of the projection across all
 880 time.

882 When predicting projections along CD_{choice} during the randomized delay task, unregularized models were used
 883 (**Fig. 3h**). This was due to the small numbers of trials for each delay length which precluded the partitioning of data
 884 into 3 separate sets (training, validation, and testing trials). Instead, models were trained with linear regression and
 885 4-fold cross-validation and tested on held-out data from each cross-validation fold. For assessing prediction quality
 886 between projections and model predictions, trials with 1.2 s delay epochs were used.

887 To understand which groups of kinematic features were most informative for predicting projections along CD_{choice},
 888 or CD_{context} (**EDFig. 3**), the absolute value of the beta coefficients for each kinematic regressor in the trained model
 889 was first obtained. For each feature group (jaw, nose, motion energy), the average beta coefficient across all
 890 regressors belonging to this kinematic feature group (8*B for jaw, 6*B for nose, and 1*B for motion energy; for
 891 example, the x and y positions and velocities for one point on the jaw on each camera totals 8 jaw regressors for
 892 each time bin, B) was calculated. The average beta coefficient for each feature group was then expressed as a
 893 fraction of the total of all beta coefficients.

894 Subspace identification (trial-averaged data)

895 Delay and Response subspaces were identified following the general approach described in ref⁴⁰. For identifying
 896 subspaces using trial-averaged data (**Fig. 5a**), neural activity was first trial-averaged separately for correct left and
 897 right trials. Activity across trial types was then concatenated, to produce a matrix $\mathbf{X} \in \mathbb{R}^{(B \cdot C) \times N}$, where B is the
 898 number of time bins, C the number of trial types, and N the number of units. Trial-averaged neural activity was
 899 soft-normalized (normalization factor=5) as described in ref⁴⁰ and subsequently baseline subtracted (baseline: -2.4
 900 to -2.2 s before go cue, during the ITI) The matrix, \mathbf{X} , was further divided into two matrices, \mathbf{X}_{delay} and $\mathbf{X}_{response}$. \mathbf{X}_{delay}
 901 contained activity from [-1,0] seconds relative to the go cue, and $\mathbf{X}_{response}$ contained activity from [0,1] seconds
 902 relative to the go cue. Delay and response subspaces were then identified by solving the following optimization
 903 problem:

904
 905
$$[\hat{\mathbf{Q}}_{delay}, \hat{\mathbf{Q}}_{response}]$$

 906
$$= \underset{[\mathbf{Q}_{delay}, \mathbf{Q}_{response}]}{\operatorname{argmax}} \frac{1}{2} \frac{\operatorname{Tr}(\mathbf{Q}_{delay}^T \mathbf{C}_{delay} \mathbf{Q}_{delay})}{\sum_{i=1}^{d_{delay}} \sigma_{delay}(i)} + \frac{1}{2} \frac{\operatorname{Tr}(\mathbf{Q}_{response}^T \mathbf{C}_{response} \mathbf{Q}_{response})}{\sum_{i=1}^{d_{response}} \sigma_{response}(i)}$$

 907
 908
$$\text{subject to } \mathbf{Q}_{delay}^T \mathbf{Q}_{response} = 0, \quad \mathbf{Q}_{delay}^T \mathbf{Q}_{delay} = I, \quad \mathbf{Q}_{response}^T \mathbf{Q}_{response} = I$$

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where C_{delay} and $C_{response}$ are the covariances of X_{delay} and $X_{response}$, σ_{delay} and $\sigma_{response}$ are the singular values of C_{delay} and $C_{response}$, and d_{delay} and $d_{response}$ are the dimensionality of the subspaces. This optimization problem jointly identifies the subspaces that maximally contain the variance in neural activity during the delay and response epochs. The dimensionality of each space was chosen to be half the number of simultaneously recorded neurons, or twenty, whichever was smaller. Therefore, the dimensionality of the full population was equal to the dimensionality of the delay or response subspaces for sessions containing forty or fewer neurons. Optimization was performed using the `manopt`¹⁰⁷ toolbox for MATLAB.

918 Subspace identification (single-trial data)

919 For identifying subspaces using single-trial data (**Fig 5h**), single-trial neural activity was first binned in 5 ms
920 intervals and smoothed with a causal Gaussian kernel with a half width of 35 ms. Each trial's activity was subtracted
921 by the average baseline activity across trials and scaled by the standard deviation across trials (baseline: -2.4 to -2.2
922 s before go cue, during the ITI). $X_{moving} \in \mathbb{R}^{B_p \times N}$ and $X_{stationary} \in \mathbb{R}^{B_n \times N}$ were defined using the single trial neural
923 activity when the animal was moving or stationary (see **Motion Energy**), respectively. B_n was the number of time
924 bins during which the animal was annotated as stationary and B_p the number of time points annotated as moving.
925 All correct and error trials from DR and WC contexts were used unless specified otherwise. Once the data was
926 partitioned into moving and stationary time points, subspace identification was carried as described for trial-
927 averaged data in the preceding paragraph:

928
929

$$\begin{aligned} & [\hat{Q}_{mov-null}, \hat{Q}_{mov-pot}] \\ & = \underset{[Q_{mov-null}, Q_{mov-pot}]}{\operatorname{argmax}} \frac{1}{2} \frac{\operatorname{Tr}(Q_{mov-null}^T C_{stationary} Q_{mov-null})}{\sum_{i=1}^{d_{mov-null}} \sigma_{stationary}(i)} \\ & + \frac{1}{2} \frac{\operatorname{Tr}(Q_{mov-pot}^T C_{moving} Q_{mov-pot})}{\sum_{i=1}^{d_{mov-pot}} \sigma_{moving}(i)} \end{aligned}$$

930
931
932

$$\text{subject to } Q_{mov-null}^T Q_{mov-pot} = 0, \quad Q_{mov-null}^T Q_{mov-null} = I, \quad Q_{mov-pot}^T Q_{mov-pot} = I$$

933
934

935 We quantified the normalized variance explained in a subspace as in refs^{40,108} (**Fig. 5d,k**):

936

$$\text{normVE} = \frac{\operatorname{Tr}(Q^T C Q)}{\sum_{i=1}^d \sigma(i)}$$

937
938

939 where Q is the subspace, C is the covariance of neural activity, and σ are the singular values of C . This normalization
940 provides the maximum variance that can be captured by d dimensions.

941
942

Unit activity was reconstructed from movement-null and movement-potent subspaces according to the following
equation:

943
944
945
946

$$X_{subspace} = X Q^T$$

$$X_{recon} = X_{subspace} Q$$

947
948
949

where X_{recon} is the reconstructed neural activity, $X_{subspace}$ is the projected neural activity within the movement-null
or movement-potent subspace, X is either single-trial or trial-averaged firing rates and Q is either the movement-
null or movement-potent subspace.

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Bootstrapped distributions of coding directions within the movement-null and movement-potent subspaces were
obtained through two separate methods. For **Fig. 7** and **EDFig. 7a,c**, we first estimated movement-null and
movement-potent subspaces per session and reconstructed neural activity from each subspace. Then, we performed
the hierarchical bootstrapping procedure as described in **Hierarchical bootstrapping**. For each iteration, we used
the original neural activity to estimate the coding directions and then projected the reconstructed neural activity

955 onto the coding directions. For **EDFig. 5b**, for each bootstrap iteration, the reconstructed neural activity itself was
956 used to estimate the coding directions. Activity within each subspace was then projected along the respective coding
957 directions. For **Fig. 7b,f**, coding directions were directly identified from the reconstructed neural activity, $\mathbf{X}_{\text{recon}}$, for
958 the individual example sessions.

959 Subspace alignment for an individual unit was calculated as:

960

$$961 \quad A = \frac{VE_{\text{mov-null}} - VE_{\text{mov-pot}}}{VE_{\text{mov-null}} + VE_{\text{mov-pot}}}$$

962 where VE is the variance explained of each individual unit by the movement-null or movement-potent subspace, or
963 by the activity along a coding direction within the movement-null or movement-potent subspace. VE for a single
964 unit was calculated as:

965

$$966 \quad VE = 1 - \frac{\sum_t (\mathbf{x}_t - \hat{\mathbf{x}}_t)^2}{\sum_t (\mathbf{x}_t - \bar{\mathbf{x}})^2}$$

967

968 where \mathbf{x}_t is the trial-averaged firing rate, $\hat{\mathbf{x}}$ is the reconstructed trial-averaged firing rate, and t is the time bin.

970 To ask if the number of single units observed to be aligned to either the movement-null or movement-potent
971 subspace was different than expected by chance, we compared the distributions to those obtained from randomly
972 sampled subspaces as described in ref⁴⁰. Each element comprising a subspace was randomly sampled from a normal
973 distribution with zero mean and unit variance but was biased by the covariance structure of the neural activity for a
974 given session. Biasing the randomly sampled subspaces by the covariances controls for the unbalanced variance
975 between stationary and moving time points (or between delay and response epochs). That is to say that the shuffled
976 distributions take into account the relative amount of movement tuning across the neural population.

977 We sampled random subspaces, $\mathbf{v}_{\text{mov-null}}$ and $\mathbf{v}_{\text{mov-pot}}$ as follows:

978

$$\mathbf{v}_{\text{mov-null}} = \text{orth} \left(\frac{\mathbf{U}_{\text{mov-null}} \sqrt{\mathbf{S}_{\text{mov-null}}} \mathbf{v}}{\|\mathbf{U}_{\text{mov-null}} \sqrt{\mathbf{S}_{\text{mov-null}}} \mathbf{v}\|_2} \right)$$

979

$$\mathbf{v}_{\text{mov-potent}} = \text{orth} \left(\frac{\mathbf{U}_{\text{mov-pot}} \sqrt{\mathbf{S}_{\text{mov-pot}}} \mathbf{v}}{\|\mathbf{U}_{\text{mov-pot}} \sqrt{\mathbf{S}_{\text{mov-pot}}} \mathbf{v}\|_2} \right)$$

980 Where \mathbf{U} and \mathbf{S} are the left and right singular vectors of their associated covariance matrices, $\mathbf{C}_{\text{stationary}}$ and $\mathbf{C}_{\text{moving}}$,
981 and \mathbf{v} is a matrix whose elements are independently drawn from a normal distribution with zero mean and unit
982 variance. As described above, covariance matrices $\mathbf{C}_{\text{stationary}}$ and $\mathbf{C}_{\text{moving}}$ are defined by neural activity during
983 stationary and movement time points for single trial data. $\text{orth}(\mathbf{A})$ computes the orthonormal basis of a matrix \mathbf{A} .
984 Neural activity from each session was projected along the randomly sampled subspaces and alignment indices were
985 calculated. This procedure was repeated 1000 times to generate null distributions, which represents the alignment
986 indices of our data with random subspaces (**EDFig. 5**). To generate p -values associated with **Fig. 5n**, **Fig. 7d,h**,
987 **and Fig. 8d**, on each iteration, we computed the proportion of strongly tuned units (alignment ≥ 0.8 and alignment
988 ≤ -0.8). This provided two distributions, one for alignment ≥ 0.8 and another for alignment ≤ -0.8 . These chance
989 distributions were separately fit with gaussian distributions using the `fitgmdist()` function in MATLAB. Then, p -
990 values were computed as the probability of observing the proportion of tuned units we observe in the data from the
991 fitted distributions.

992 Subspaces were identified using data from DR and WC correct and error trials (**Fig. 5,7, and 8**). Control analyses
993 were performed using separate sets of trials to assess if the movement-potent subspace erroneously contained
994 movement-null-subspace dynamics. First, we estimated subspaces using WC trials only (**EDFigs. 4 and 8**). Second,
995 we estimated subspaces using DR and WC trials, but restricted time points used to those in the response epoch only
996 (**EDFigs. 4 and 8**). Both controls allowed us to estimate movement-null and movement-potent subspaces in the
997 presence of uninstructed movements, but in the absence of planning dynamics. These controls thus allowed us to
998 measure the degree to which the movement-potent subspace erroneously captured movement-null dynamics.

In a further attempt to validate that the movement-potent subspace is not inadvertently capturing movement-correlated internal dynamics, we identified movement-null and movement-potent subspaces using a two-stage PCA approach (**EDFig. 4**). The movement-null subspace was first identified as the dominant principal components (first 5 PCs) of the single-trial firing rates when mice are not moving. Second, the activity within the movement-null subspace was removed from single-trial firing rates. Then, the movement-potent subspace was calculated as the first 5 PCs of the single-trial residuals:

$$\mathbf{X}_{mov-null} = \mathbf{X}\mathbf{Q}_{mov-null}^T$$

$$\mathbf{X}_{recon,mov-null} = \mathbf{X}_{mov-null}\mathbf{Q}_{mov-null}$$

$$\mathbf{Q}_{mov-pot} = PCA(\mathbf{X} - \mathbf{X}_{recon,mov-null})$$

$$\mathbf{X}_{mov-pot} = \mathbf{X}\mathbf{Q}_{mov-pot}^T$$

$\mathbf{X} \in \mathbb{R}^{(B \times K) \times N}$ is the single-trial firing rates where B is the number of time points, K the number of trials, and N the number of units. $\mathbf{Q}_{mov-null}$ is the first 5 PCs of the single-trial firing rates when animals are stationary, and $\mathbf{X}_{mov-null}$ is the projection along those PCs. $\mathbf{X}_{recon,mov-null}$ is the reconstructed neural activity obtained from the multiplication of activity within the movement-null subspace, $\mathbf{X}_{mov-null}$, and the movement-null subspace, $\mathbf{Q}_{mov-null}$. $PCA(\mathbf{Z})$ indicates computing the PCs of the matrix \mathbf{Z} . $\mathbf{Q}_{mov-pot}$ is the first 5 PCs of the single-trial residuals obtained from subtracting $\mathbf{X}_{mov-null}$ from the single-trial firing rates, \mathbf{X} . Finally, $\mathbf{X}_{mov-pot}$ is obtained from projecting single-trial firing rates onto $\mathbf{Q}_{mov-pot}$. $\mathbf{X}_{recon,mov-null}$ contains activity that is explainable by the first 5 PCs in the absence of movement and, therefore, the residuals contain movement-related neural dynamics. Thus, performing PCA on these residuals provides a movement-potent subspace that is orthogonal to the movement-null subspace. This approach ensures dynamics observed during stationarity are contained within the movement-null subspace prior to assigning any dynamics to the movement-potent subspace. Therefore, it is more conservative in avoiding the mis-assignment of movement-correlated internal dynamics to the movement-potent subspace.

CD_{context} selectivity on ‘High move’ and ‘Low move’ trials

For each session, DR and WC trials were first separated into ‘High move’ and ‘Low move’ trials. ‘High move’ trials were those where the average motion energy in the ITI was greater than the movement threshold for that session (see **Motion energy**). ‘Low move’ trials were the remaining trials. The last 40 trials in each session were excluded from analysis to account for the decrease in uninstructed movements that are observed towards the end of behavioral sessions as animals become satiated and disengaged. CD_{context} was calculated from the full population or from neural activity reconstructed from either subspace. Population activity from ‘High-move’ and ‘Low-move’ trials was then projected along CD_{context}. Selectivity was defined as the trial-averaged projection along CD_{context} on DR trials minus the projection along CD_{context} on WC trials (**Fig. 8b,c**).

Hierarchical bootstrapping

Projections along coding directions were obtained via a hierarchical bootstrapping procedure^{109,110} (**Figs. 2, 7 and ED Figs. 7, 8 and 10**). Pseudopopulations were constructed by randomly sampling with replacement M mice, 2 sessions per sampled mouse, 50 correct trials of each type, 20 error trials of each type, and 20 neurons. M is the number of mice in the original cohort. Bootstrapping was repeated for 1000 iterations. In each iteration, data derived from some individual mice (and sessions, trials, and neurons) will be overrepresented and some will be omitted. Average effects driven by small subsets of animals, sessions, trials, and/or units will be accompanied by large confidence intervals. For all results obtained through this bootstrapping procedure, mean and 95% confidence intervals (shaded area) of the bootstrap distribution are shown, except for selectivity (**Fig. 7a and ED Fig. 7a**), where 5-95% confidence intervals are shown to indicate where projections significantly differ from zero ($p < 0.05$, one-sided test, bootstrap).

Statistics

No statistical methods were used to determine sample sizes. All *t*-tests were two-sided unless stated otherwise.

1049 **DATA AVAILABILITY**

1050 Primary and derived data described in this study will be made available on Figshare upon publication.

1051 **CODE AVAILABILITY**

1052 MATLAB code for subspace identification is available at <https://github.com/economolab/subspaceID>. Custom
1053 MATLAB code used for analyses will be made available on Github upon publication.

1054 **COMPETING INTERESTS**

1055 The authors declare no competing interests.

1056 **AUTHOR CONTRIBUTIONS**

1057 MAH, JEB, and MNE conceived of the project. MNE and CC supervised research. MAH, JEB, and MNE designed
1058 experiments. MAH, JEB, JLUN, and EKH performed experiments. MAH, JEB, and MNE analyzed data. MAH,
1059 JEB and MNE wrote the manuscript.

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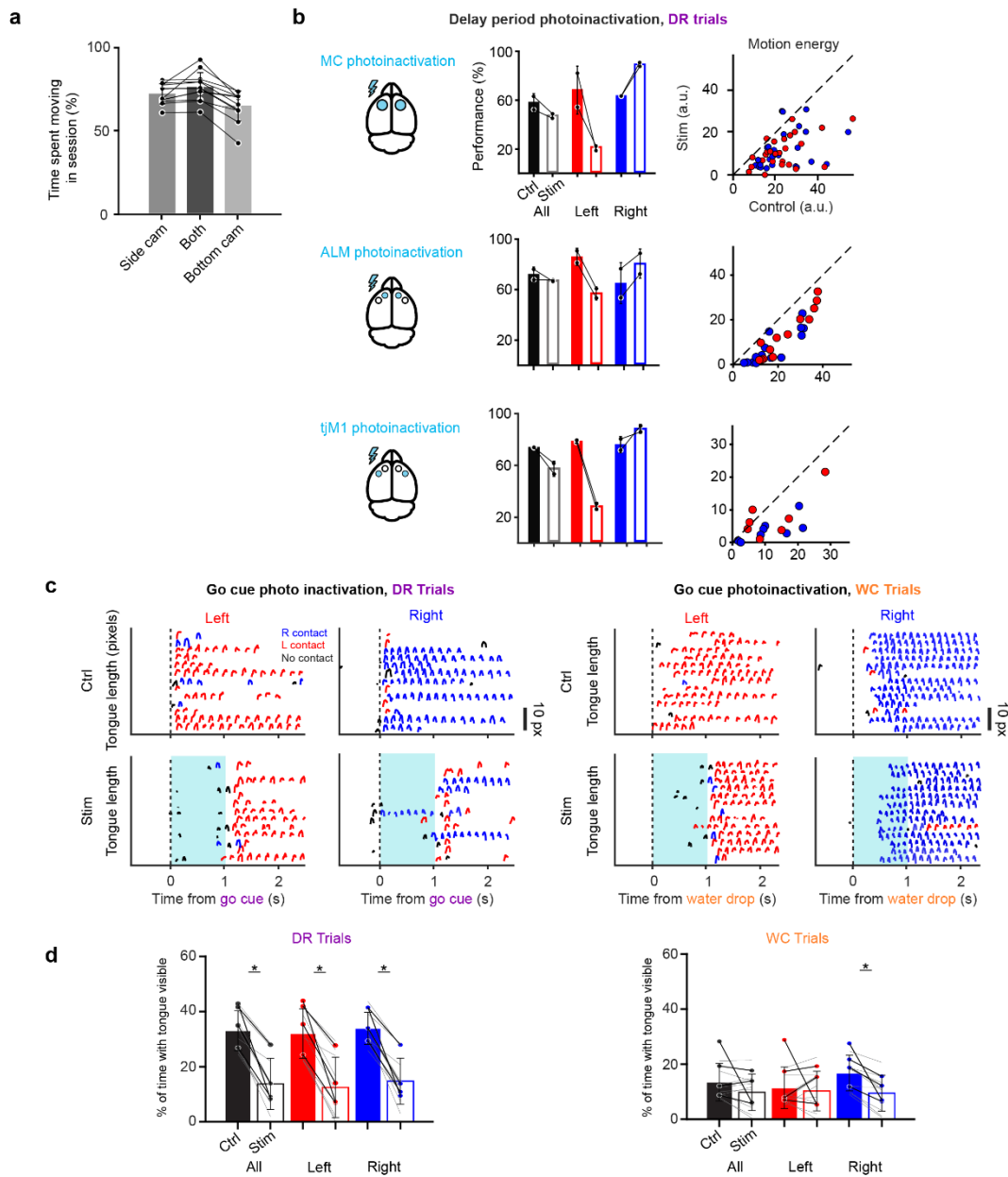
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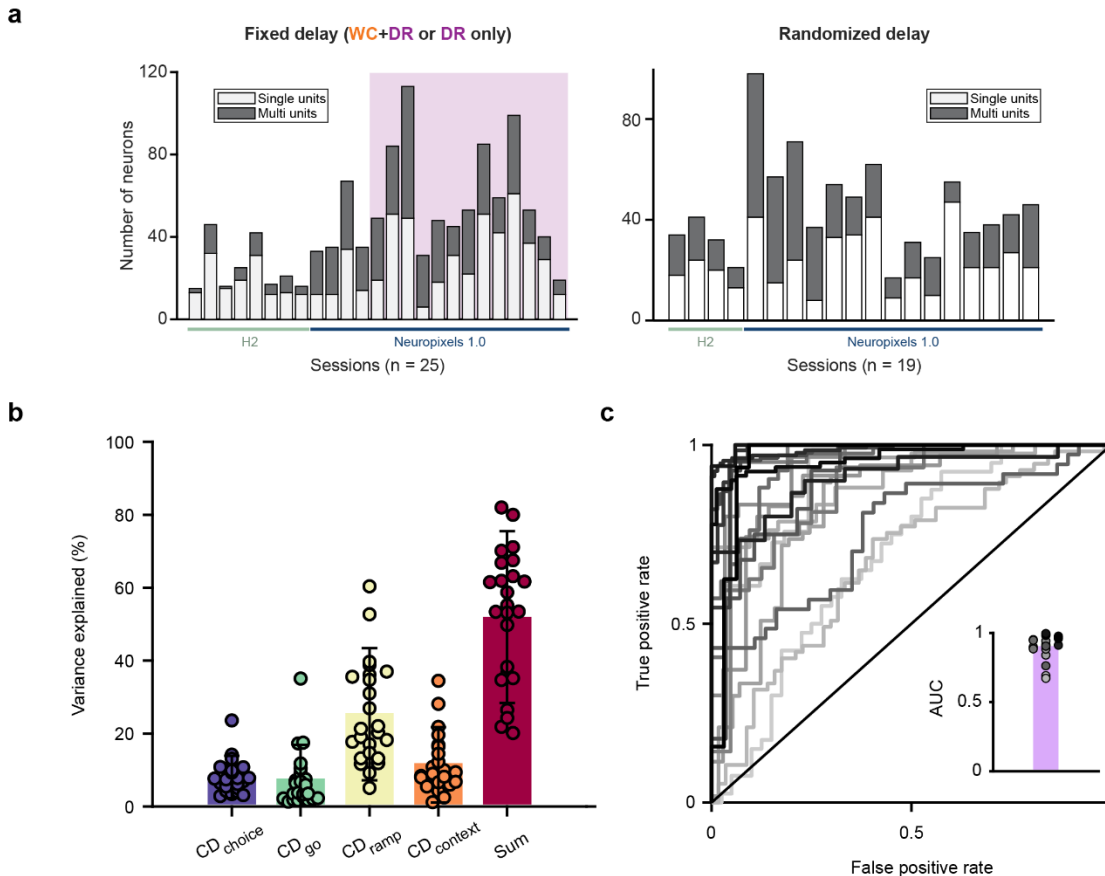
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Extended Data Fig. 1 – Region-specific photoinactivation of ALM and tJM1. **a.** Percentage of time spent moving (see **Methods**) in a session determined by video recordings using the side view, bottom view, and both views. Points indicate each of the 12 randomly selected sessions used for this analysis. **b.** Effect of delay epoch photoinactivation on behavioral performance (*middle column*) and uninstruced

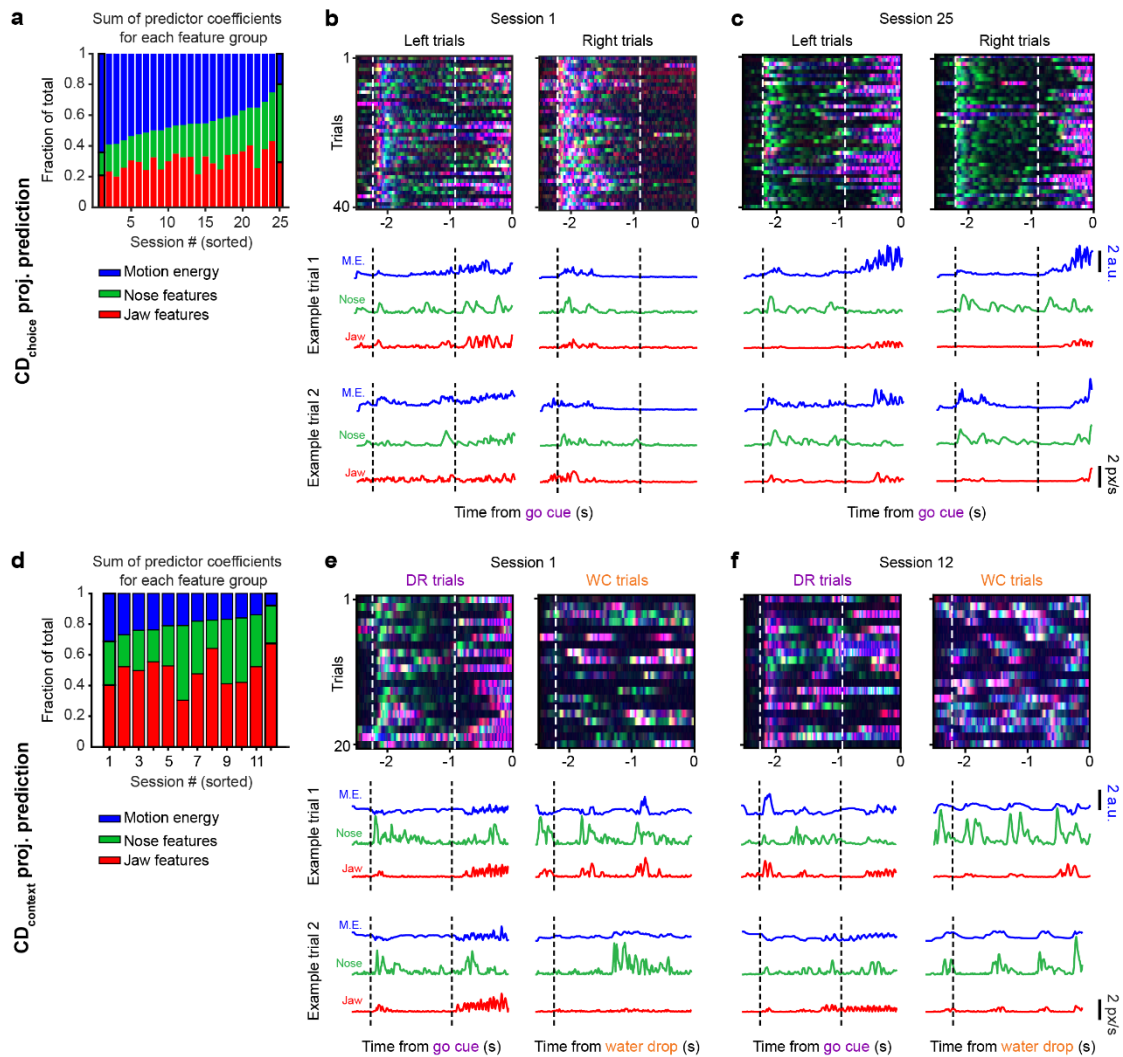
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movements (*right column*) when photoinactivation was directed to the MC (ALM + tJM1; *top row*; same data as **Fig. 1g-i**, $n = 14$ sessions, 2 mice), the ALM (*middle row*, $n = 15$ sessions, 2 mice), and the tJM1 (*bottom*, $n = 9$ sessions, 2 mice). Photoinactivation of ALM and tJM1 led to similar behavioral impairment and reduction in uninstructed movements, with larger effects observed with MC (ALM + tJM1) photoinactivation. **c.** Tongue length during control and go cue photoinactivation trials for delayed-response (*left*) and water-cued (*right*) contexts. Blue traces indicate right lickport contacts, red traces indicate left contacts, and black traces indicate no contact. Vertical dashed line indicates go cue or water drop onset. Blue shaded region indicates photoinactivation period. **d.** Percentage of time with tongue visible during photoinactivation period for DR trials (*left*) and WC trials (*right*). Each colored point indicates mean value for an animal ($n = 4$ animals), individual animals are connected by black lines. Light gray lines denote individual sessions ($n = 10$ sessions). Bars are the mean across all sessions. Asterisks denote significant differences ($p < 0.05$) between control and photoinactivation trials (Percent reduction on all DR trials: $19 \pm 7\%$, mean \pm s.d., $p = 1.6e-05$; DR left trials: $20 \pm 8\%$, $p = 3.0e-05$; DR right trials: $20 \pm 7\%$, $p = 1.6e-05$; All WC trials: $4 \pm 8\%$, $p=0.154$; WC left trials: $1\% \pm 9\%$, $p=0.702$; WC right trials: $7\% \pm 5\%$, $p=0.002$; paired t -test, $n=10$ sessions). Error bars indicate standard deviation across sessions. In WC trials, tongue protrusion was only significantly impaired on one trial type, while ability to successfully contact the lickport was impaired in all conditions (see **Fig. 1c**).



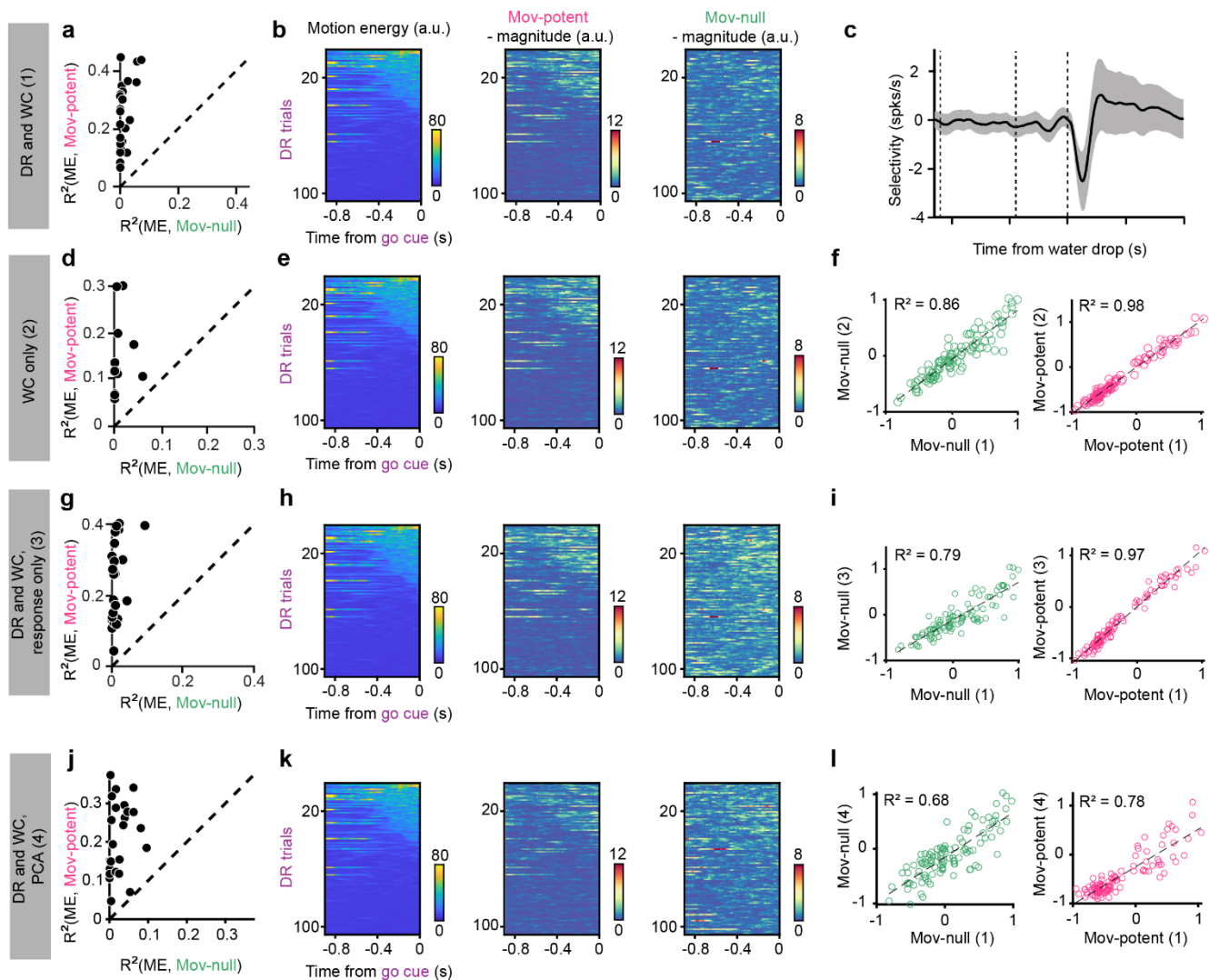
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Extended Data Fig. 2 – Session-by-session statistics. **a.** Number of recorded single- and multi-units per session for the fixed delay task (*left*) or the randomized delay task (*right*). *Left*, Purple shaded region indicates sessions in which animals only performed presented with DR trials. Green and blue bars underneath plots indicate the probe type used for a given session **b.** Variance explained of trial-averaged neural activity by each coding direction. The coding directions were calculated using neural activity from individual sessions ($n=25$). Bar height represents the mean across sessions and error bars indicate standard deviation across sessions. **c.** Receiver operating curves (ROC) demonstrating choice decoding accuracy from delay epoch CD_{choice} projections across all individual sessions (see **Methods**). Inset: area under the ROC curve (AUC). Bar height represents the mean across sessions and points indicate sessions.



1325 **Extended Data Fig. 3 - Session-by-session variability in the relationship between kinematic features and putative cognitive dynamics.**
 1326 **a.** Regression weights for each group of kinematic predictors of CD_{choice} projections, as a fraction of all predictor coefficients (see **Methods**).
 1327 Sessions are sorted in descending order by motion energy fraction. Outlined bars indicate example sessions shown in (b) and (c). **b.** Example
 1328 session where motion energy made up the largest fraction of regression weights for predicting CD_{choice} projections. *Top*, overlaid jaw/nose
 1329 speed or motion energy for a subset trials. *Bottom*, two example trials of kinematic feature trajectories. **c.** Same as (b) but for an example
 1330 session where jaw and nose features made up a larger fraction of regression weights. **d.** Same as (a) but for predicting $CD_{context}$ projections.
 1331 **e, f.** Same as (b) and (c) but for two example sessions with different regression weight fractions for predicting $CD_{context}$ projections.

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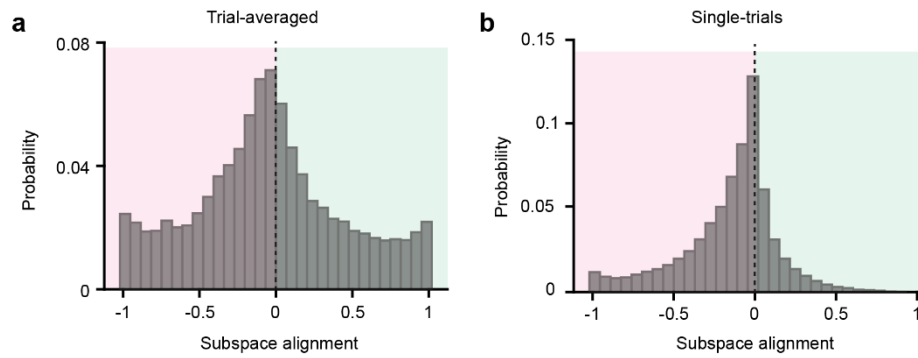
Extended Data Fig. 4 – Control analyses for subspace decomposition. **a,b.** Movement-null and movement-potent subspaces estimated as in Fig. 5g-l using DR and WC trials. **a.** Variance explained (R^2) of motion energy by the sum squared magnitude of activity in the movement-null and movement-potent subspaces on single trials. Each point is the mean across trials for a session. **b.** *Left*, motion energy on single trials for an example session. *Middle*, sum-squared magnitude of activity in the movement-potent subspace. *Right*, sum-squared magnitude of activity in the movement-null subspace. Trials sorted by average delay epoch motion energy. **c.** Selectivity (left vs. right) of the neural population during WC trials. Mean and 95% CI across sessions shown. **d,e.** Same as (a,b) but estimating movement-null and movement-potent subspaces using WC trials only. **f.** Normalized magnitude of activity in the movement-null subspace (*left*) movement-potent subspace (*right*) when estimated using DR and WC trials as in (a,b), versus when estimated using WC trials only as in (d,e). Circles are average activity per trial for an example session. **g,h.** Same as (a,b), but estimating movement-null and movement-potent subspaces using data restricted to the response epoch of DR and WC trials. **i.** Magnitude of activity in the movement-null subspace (*left*) or movement-potent subspace (*right*) when estimated using DR and WC trials as in (a,b) versus when estimated using data from only the response epoch of DR and WC trials as in (g,h). Circles are average activity per trial for an example session. **j,k.** Same as (a,b), but estimating the movement-null and movement-potent subspaces using a two-stage PCA approach (see **Methods**). This approach is conservative in avoiding the mis-assignment of cognitive dynamics that correlate in time with movement to the movement-potent subspace. **j.** Magnitude of activity in the movement-null subspace (*left*) or movement-potent subspace (*right*) when estimated using DR and WC trials as in (a,b) versus when estimated using the two-stage PCA approach as in (j,k). Circles are average activity per trial for an example session.

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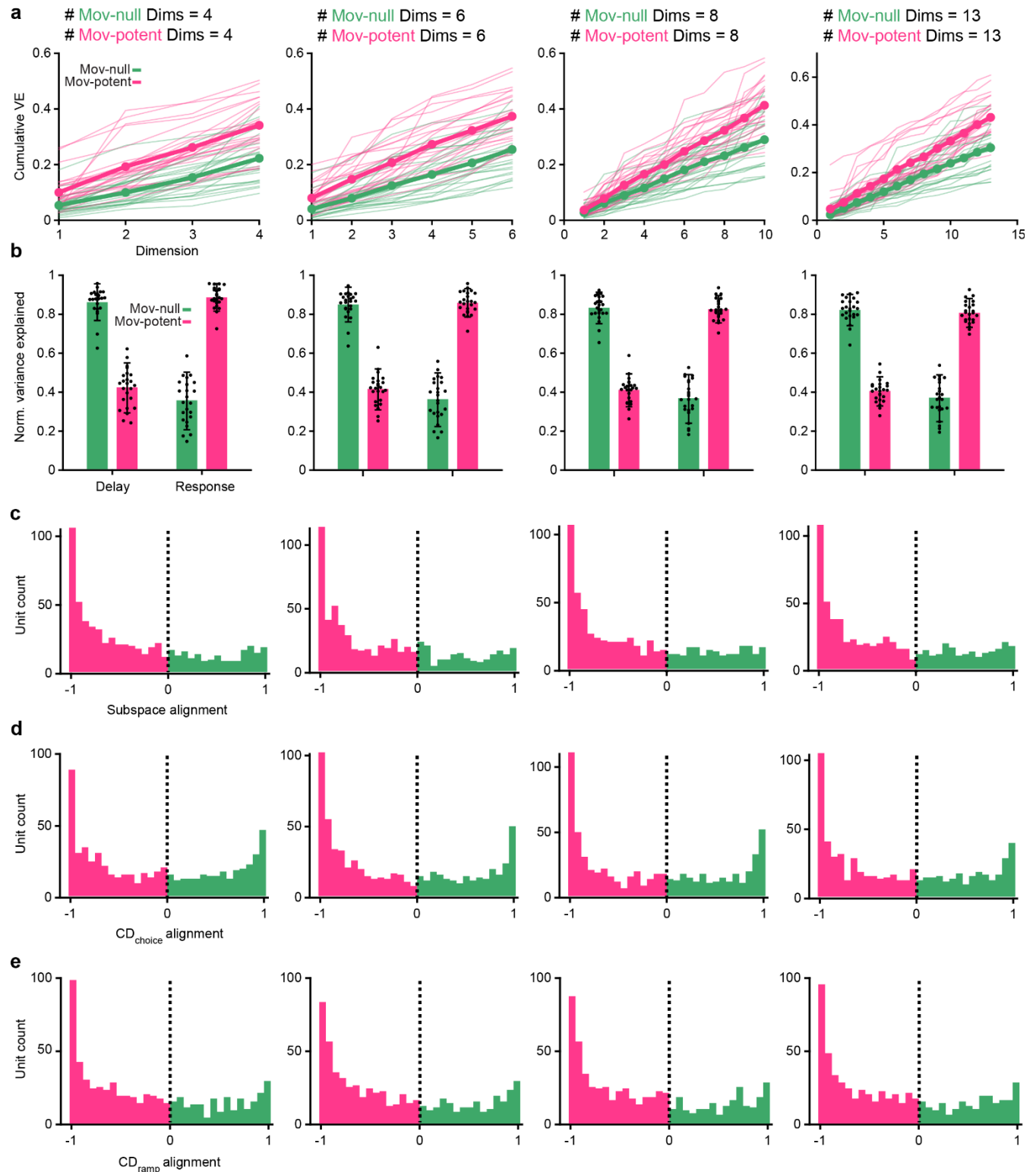
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Extended Data Fig. 5 – Alignment of single-units to random subspaces. Random subspaces were constructed by independently and identically drawing from a normal distribution with zero mean and unit variance. Each random subspace was then biased towards the covariance structure of the actual data (see **Methods**). **a.** Null distributions of alignment indices for trial-averaged data. **b.** Null distributions of alignment indices for single-trial data. Null alignment distributions are skewed towards the movement-potent subspace due to the unbalanced variance between delay and response epochs (a) or between stationary and movement time points (b), reflecting the strong movement tuning of many units.

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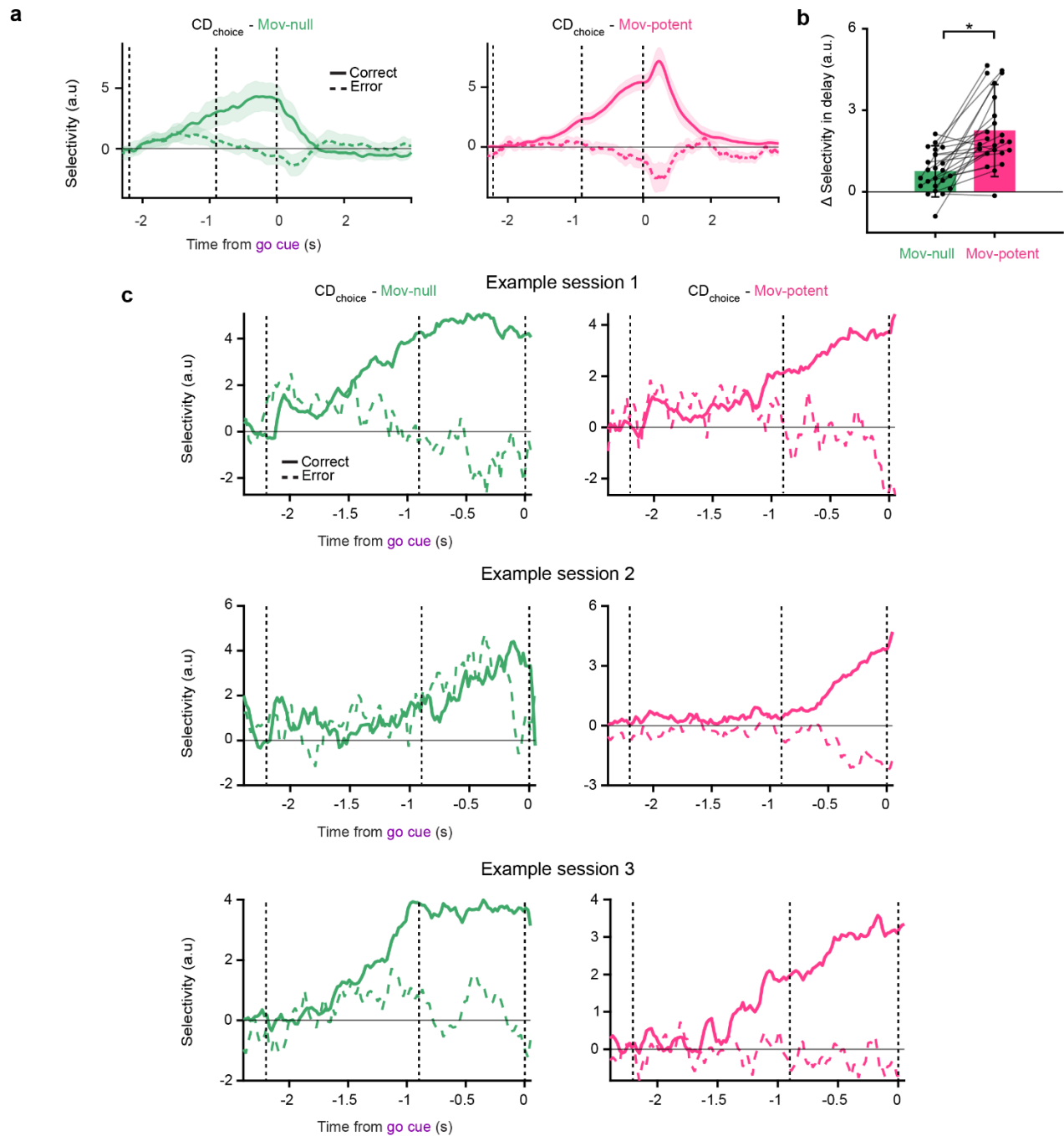
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Extended Data Fig. 6 – Varying dimensionality of subspaces. Analyses were repeated while varying the dimensionality of movement-null and movement-potent subspaces. Each subspace was constrained to be 4 (*left*), 6 (*middle left*), 8 (*middle right*), or 13 dimensions (*right*). **A.** Cumulative variance explained of the neural activity by the activity in movement-null and movement-potent subspaces. Bold lines and points indicate mean across sessions. Thin lines represent single sessions **b.** Normalized variance explained of neural activity during the delay or response epoch by the activity in movement-null and movement-potent subspaces. Points indicate sessions, bar height indicates mean across sessions, and error bars indicate standard deviation across sessions (n=25 sessions). **c-e.** Subspace (**c**), CD_{choice} (**d**), and CD_{ramp} (**e**) alignment distributions when varying dimensionalities of each subspace.



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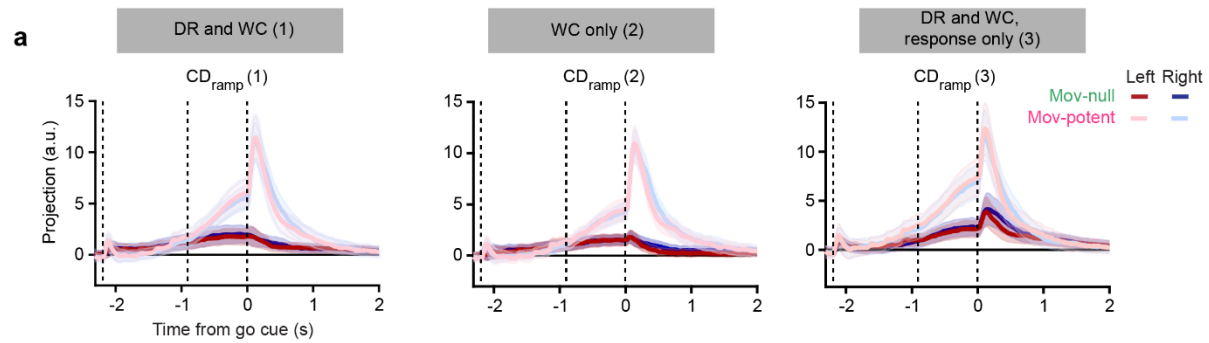
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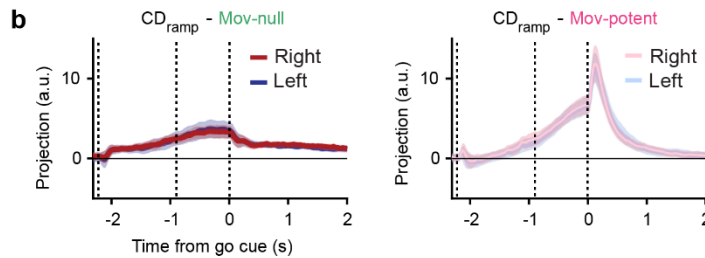
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Extended Data Fig. 7 – Projections along movement-null and movement-potent components of CD_{choice}. **a.** Same data as in **Fig. 7a** except all time in trial shown to highlight activity during the response epoch. Selectivity (projections onto CD_{choice} on lick-right trials minus projections on lick-left trials) of movement-null (*left*) and movement-potent (*right*) subspace activity. Mean and 5-95% CI of the bootstrap distribution for correct (*solid*) and error (*dashed*) trials shown. **b.** Change in selectivity between the last 100ms of the delay epoch and the last 100ms of the sample epoch in movement-null and movement-potent components of projections along CD_{choice} (Movement-potent: 2.25 ± 1.57 , mean \pm s.d., Movement-null: 0.76 ± 0.8 , $p=1 \times 10^{-5}$, paired *t*-test, $n = 25$ sessions). Points indicate individual sessions, bar height indicates mean across sessions, and error bars indicate standard deviation across sessions. **c.** Three example sessions from three different mice depicting selectivity along CD_{choice} as in **Fig. 7a**. Solid lines denote the mean projection on correct trials and dashed lines denote the mean projection error trials.



Determining CD_{ramp} using activity from reconstructed activity from movement-null and movement-potent subspaces



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Extended Data Fig. 8 – Within-subspace CD projections using variations on procedure to determine subspaces. **a.** Projections of movement-null and movement-potent subspace activity along CD_{ramp} for each of three analytical variations. Movement-null and movement-potent subspaces were identified using both DR and WC trials (*left*), WC trials only (*middle*), and the response epoch of DR and WC trials (*right*). Mean and 95% CI of bootstrap distribution shown. **b.** Projections along movement-null (*left*) and movement-potent (*right*) components of CD_{ramp} when determined from activity within each subspace individually, rather than from the full neural population. Mean and 95% CI of bootstrap distribution shown.

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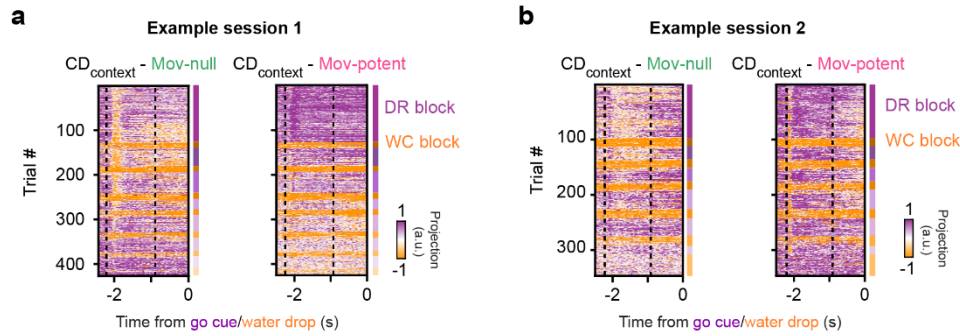
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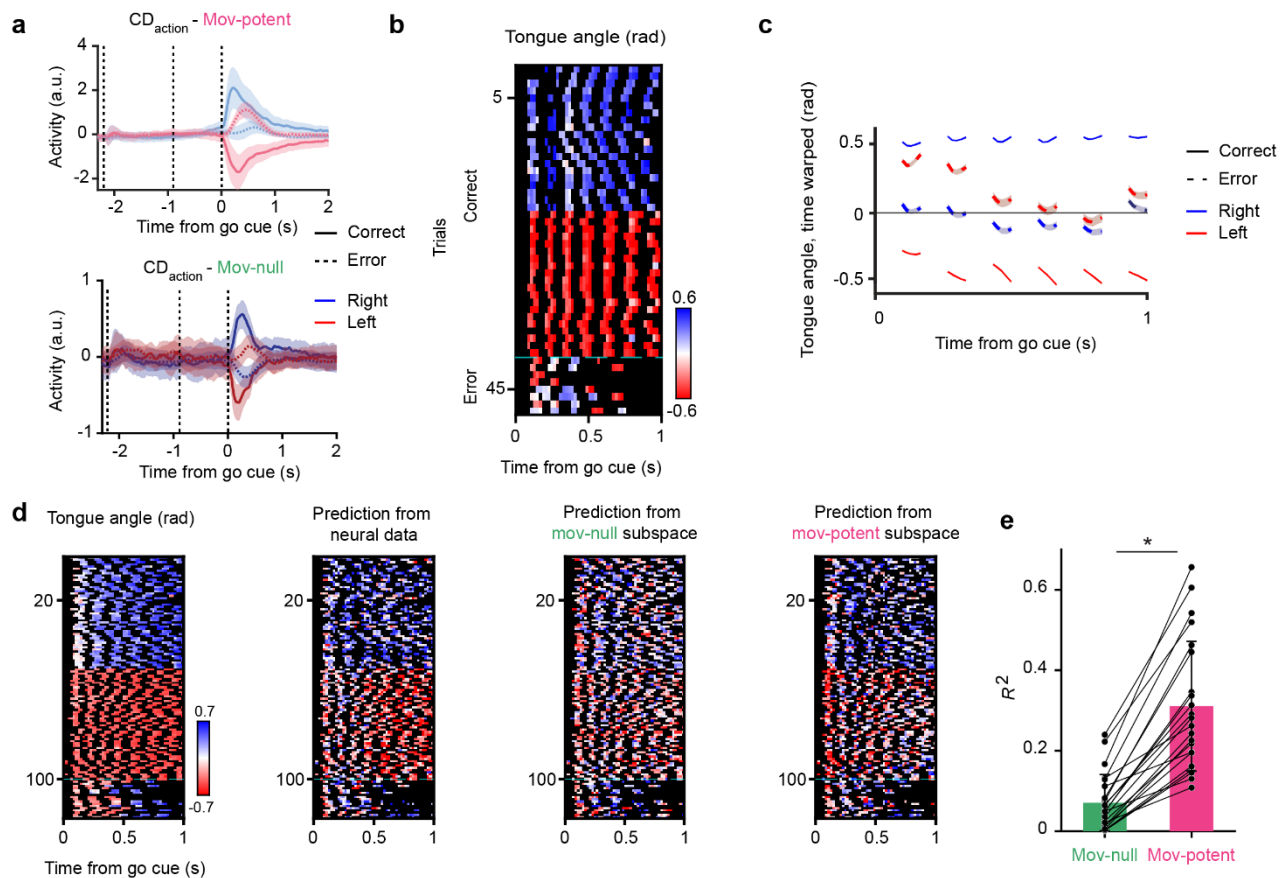
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Extended Data Fig. 9 – Encoding of context in both the null and potent subspaces tracks block-wise task structure. a. Heatmap of single-trial projections of null and potent subspace activity along CD_{context} for an example session. The chronological DR or WC block within the session is denoted by differently shaded purple and orange rectangles, respectively, on the right of each plot. **b.** Same as (a) but for another example session, from a different animal.

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1423 **Extended Data Fig. 10 – Relationship between tongue angle and neural activity in the movement-null and movement-potent**
 1424 **subspaces.** **a.** Projections along movement-potent (*top*) and movement-null (*bottom*) components of CD_{action} . Correct trials shown in solid
 1425 lines and error trials shown in dashed lines. **b.** Tongue angle for an example session for correct and error trials. Black values indicate tongue
 1426 not visible. **c.** Tongue angle on correct and error right and left trials. Tongue angle was linearly time warped to allow for averaging over trials
 1427 and sessions. Mean and s.e.m. across sessions shown. **d.** Tongue angle (*left*) and predictions from the full population neural activity (*middle*
 1428 *left*), null subspace activity (*middle right*), and potent subspace activity (*right*) for an example session. **e.** Variance explained (R^2) of tongue
 1429 angle by prediction from movement-null (*green*) and movement-potent (*pink*) subspaces. Asterisks denote significant differences between
 1430 predictions from null and potent subspaces ($p=2 \times 10^{-8}$, paired t-test, $n=25$ sessions).

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1432 **Supplementary Movie 1 – Uninstructed movements vary in their identity and timing.** Example trials in which uninstructed movements
 1433 vary in their identity (across rows) and timing (across columns). Traces represent the y-position of the feature within the video frame. All
 1434 example trials taken from the same mouse and session.

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